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Systematic Zoology

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Zoogeography of the Near East

CURT KOSSWIG

EVEN though Anatolia (that is, Asia Minor and the neighboring eastern region called East Anatolia, in so far as it is a part of the Turkish Republic) can be included in the Palaearctic region, the number of faunistic elements of other than Palaearctic origin and/or distribution is highly remarkable. The same is true for Syria and Palestine, although the influence of Oriental and Aethiopian elements is much more noticeable in Palestine than in Anatolia. This means that there is a gradient from north to south for Palaearctic forms in the region in question.

It seems quite natural that in the distribution of animals there is not a clear-cut faunistic boundary but merely a more or less gliding transition from the center of one faunistic region to that of another. Unfortunately, how much significance an author is ready to attribute to the transitional character of a given region is a question of rather subjective judgement. From the point of view of the zoogeographer interested in Lepidoptera it may be justifiable to deny the transitional character of the Anatolia-Palestine region because the dominance of Palaearctic elements even down to North Africa is so well established that the intermingling into this fauna of some Aethiopian wandering species or of Eremian forms in the warm steppes or the deserts of this zone can practically be neglected. For the modern lepidopterist only the distribution of the different subspecies of a certain species is of importance; the area occupied by the different subspecies is, most probably, the result of the postglacial expansion from some refuges during the glaciation. De Lattin (1951-1952) worked out this interesting problem with great care and success.

It is easily understandable that the degree of certainty in reconstructing the historical geography of an area or of a species rises with approximation to present-day conditions. The more we have to refer to the geological past for the understanding of the present distribution of a systematic unit, the more hypothetical becomes our reconstruction of the probable historical course of events. At the same time, a higher degree of systematic independence among the forms compared means a diminished probability that their groupings are really natural. Whereas it can be taken for granted that all subspecies of one modern species are derived from one common ancestor, we can never be so sure when we compare different species or higher systematic units. In the ideal case a good (that is, a natural) system has to correspond to the degree of natural affinity; but we have to admit that in many cases there is still uncertainty about the natural relationship between species included in the same genus or between genera included in the same family. There are, however, many examples in which, for the understanding of the present distribution of a systematic unit, not the degree of relationship between certain members of this unit but the area covered by it actually and/or in the past is of primary importance. Fortunately in many such cases, facts concerning the biology and ecology of the form or group under investigation can be used as complementary to our deficient or uncertain systematic knowledge. The following pages may be understood from this point of view.

Faunal Boundary

A relatively sharp boundary between a fauna with many typically Palaearctic representatives and another of different faunistic relationship can be observed the

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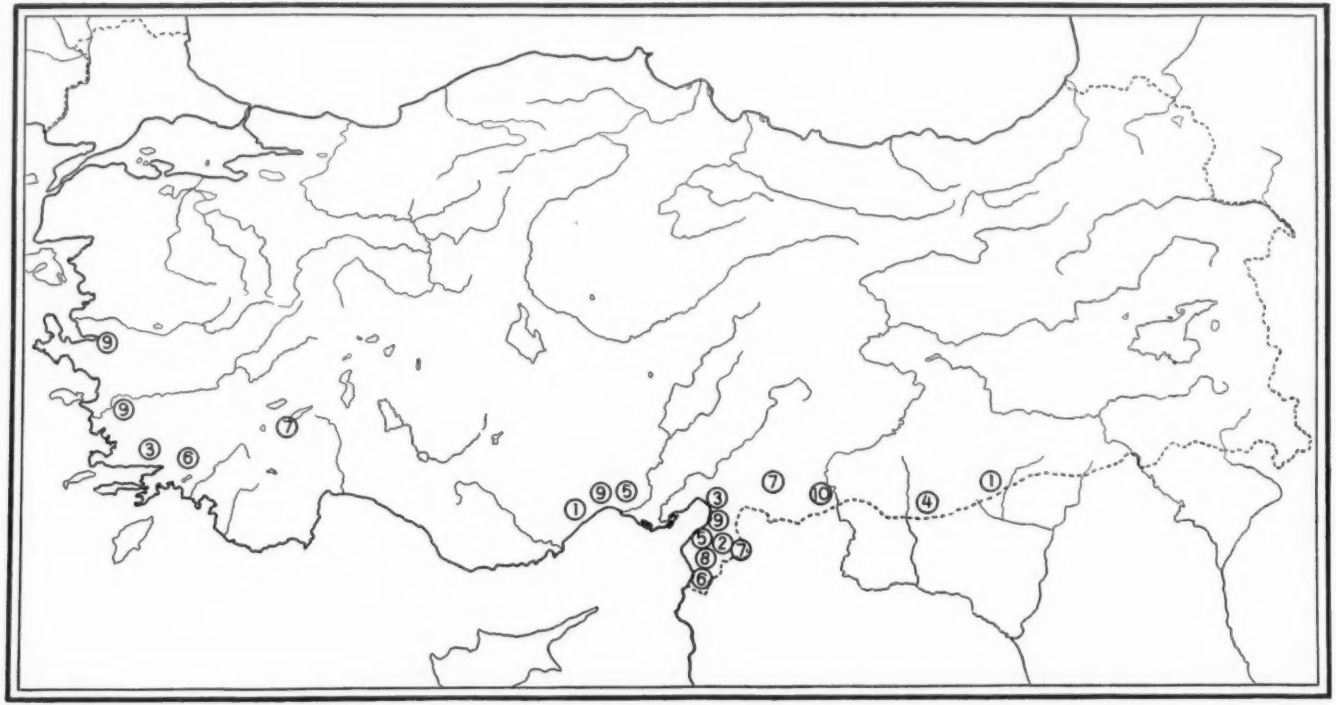

FIG. 1. Distribution of species of preferentially tropical distribution. 1. Driver ant, *Dorylus punicus*. 2–4. mammals: 2. *Rousettus aegyptus;* 3. *Herpestes ichneumon;* 4. *Gazella dorcas*. 5–8 and 10. birds: 5. *Pycnonotus xanthopygus;* 6. *Halcyon smyrnensis;* 7. *Ceryle rudis;* 8. *Anhinga rufa* (*chantrei*); 10. *Comatibis eremita*. 9. Chameleon (*Chamaeleo chamaeleo*).

moment we enter the plains south of the Toros mountains (Fig. 12). Suddenly one feels oneself in a foreign country, among an unfamiliar fauna from the central or eastern Anatolian steppes, or from the mountainous regions of northern, eastern, or western Anatolia. Animals such as driver ants (*Dorylus punicus*), fruit-eating bats (*Rousettus aegyptus*), the mysterious darter (*Anhinga rufa chantrei*), bülbüls (*Pycnonotus xanthopygus*), soft-skinned tortoises (*Trionyx euphratica*), a large monitor (*Varanus griseus*), the mongoose (*Herpestes ichneumon*), the saphan of the Bible (*Hyrax syriacus*), and many other species well known in Palestine find their northern limit on the southern slopes of the Toros mountains. We have good reason to assume that these species are newcomers in the south Anatolian fauna, having intruded into the north as late as the end of the glacial epoch. The specific and racial identity of many of these elements, with their congeners in Palestine and farther to the south, in Africa or in India proves this fact. (Figs. 1, 2.)

On the other hand, as a result of a movement towards the south in the glacial (pluvial) periods, some species that are widely distributed in Anatolia and even more in the north, e.g. in the Caucasus, the Balkans, Alps, or Central Europe, still exist in Syria and/or Palestine. Representatives of this element of more northern origin are, among others (Bodenheimer, 1935), the fire salamander, *Salamandra salamandra*, the newt *Tritu-*

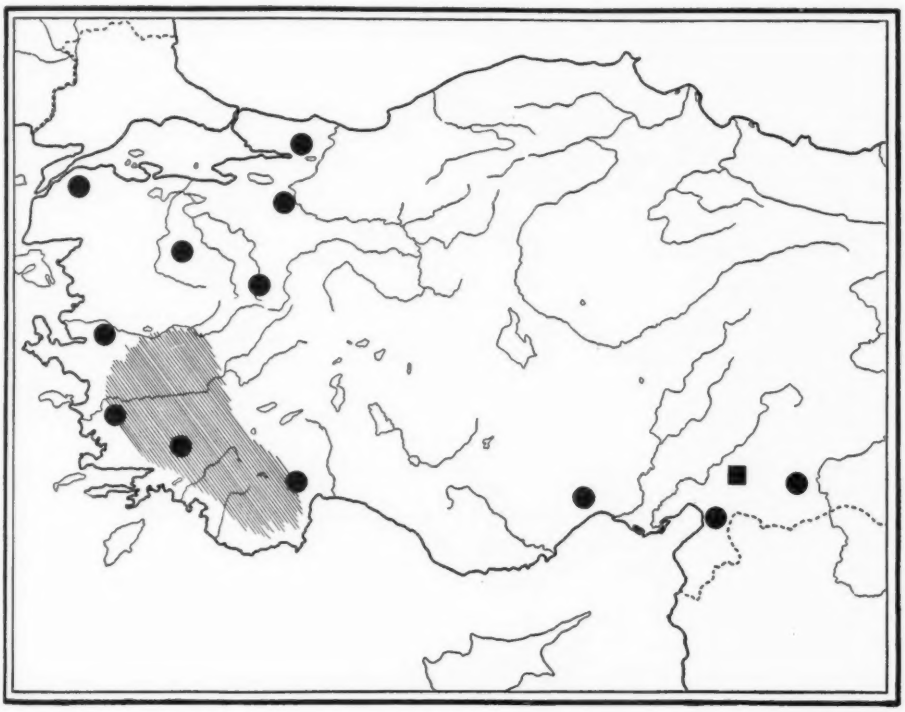

FIG. 2. Warmth-loving mammals in Anatolia. *Hystrix hirsutirostris* is indicated by circles. The area of *Felis pardus tullianus* is indicated by shading; one place at the eastern border of Asia Minor is indicated by a square.

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rus vittatus, in earlier times the roe deer, and even some freshwater fish like *Alburnus, Rutilus,* and *Cobitis* (Fig. 3). Other intruders of northern origin, the Angara element, arrived together with the forms preferring cold and humidity mentioned above. The Angara element confronts us with species of the cold steppes of eastern Siberia which in glacial times easily gained distribution towards the west and from there also to the south. Grasshoppers of the genera *Stenobothrus* and *Chorthippus,* well represented in Anatolia, in the steppes as well as in the high mountainous regions, can be cited here. They can be found in some forms as far to the south as Palestine. Some other animals of Palaearctic origin, carabid beetles for example, and an earwig of the *Forficula tomis* group even reached tropical Africa where they are mostly confined today to the high mountain regions of East Africa.

The southern movement to Africa in glacial-pluvial times was facilitated by some land-bridges between the Palaearctic and Aethiopian regions, of which the one going through Syria and Palestine seems to have been very important. As a general rule we can state that there is a gradient from north to south in such a way that the Palaearctic forms become rarer the further we go towards the south. Today there are some discontinuities in this gradient caused by local ecological situations in certain regions that were passable in former periods.

An inverse gradient from south to north exists for tropical elements, and in this case again local ecological reasons rather than historical ones seem to have determined the absence of some forms, where their existence could be expected. For example, the fact that no mouth-breeding cichlid fish (*Tristramella*) can be found in the lake of Antiochia, whereas they exist in Aleppo, may be caused, not by the restricted mobility of these fish, but by some special ecological factor not known to us as yet.

This exchange of representatives of land and freshwater faunas of different origin, the one coming from the modern tropics, the other developing in the Palaearctic, began in the Pliocene. In this geological period the last communication between the Mediterranean Sea and the Indian Ocean, the so-called Syrian-Iranian Sea, retired completely, allowing the migration farther to the south, and conversely to the north, of land and freshwater animals. Until the desiccation of the Syrian-Iranian Sea, the Anatolian fauna developed primarily as a part of the Palaearctic fauna. Bodenheimer suggests (1935) in a more special sense that a great part of the Anatolian fauna in the Tertiary derived from what he calls the Atlantic fauna, in which the Mediterranean region and some of the Atlantic islands are to be included. In fact, there is a most remarkable similarity in the composition of the faunal elements in Anatolia, the peri-Mediterranean and the sub-Mediterranean regions, especially in groups with restricted mobility like millipedes, woodlice (Verhoeff, 1940, 1941*a*, 1941*b*), and also others. Families of animals of slow mobility, active or passive, such as the millipedes, offer an excellent material for historical zoogeography (Kosswig, 1943). In contrast to the millipedes of Anatolia, which show a preponderant Palaearctic, Mediterranean, or sub-Mediterranean, relationship, those of Palestine reveal relations also with Africa by the presence of spirostreptids completely absent even in the most southern regions of Turkey. But it seems worth mentioning that a remarkably high number of the diplopods of Palestine show near relationship with those of the Caucasus and of Anatolia (e.g. genera *Amblyiulus, Brölemannia, Lysiopetalum*). The distribution towards the south of these elements is nearly in correspondence with that of the genera *Salamandra* and *Triturus.* In the southernmost corner of Turkey, in the Sandjak of Iskenderun a glomerid was found which has its nearest relative (Dr. Lohmander in litt.) in *Albanoglomis,* a western Balkan genus.

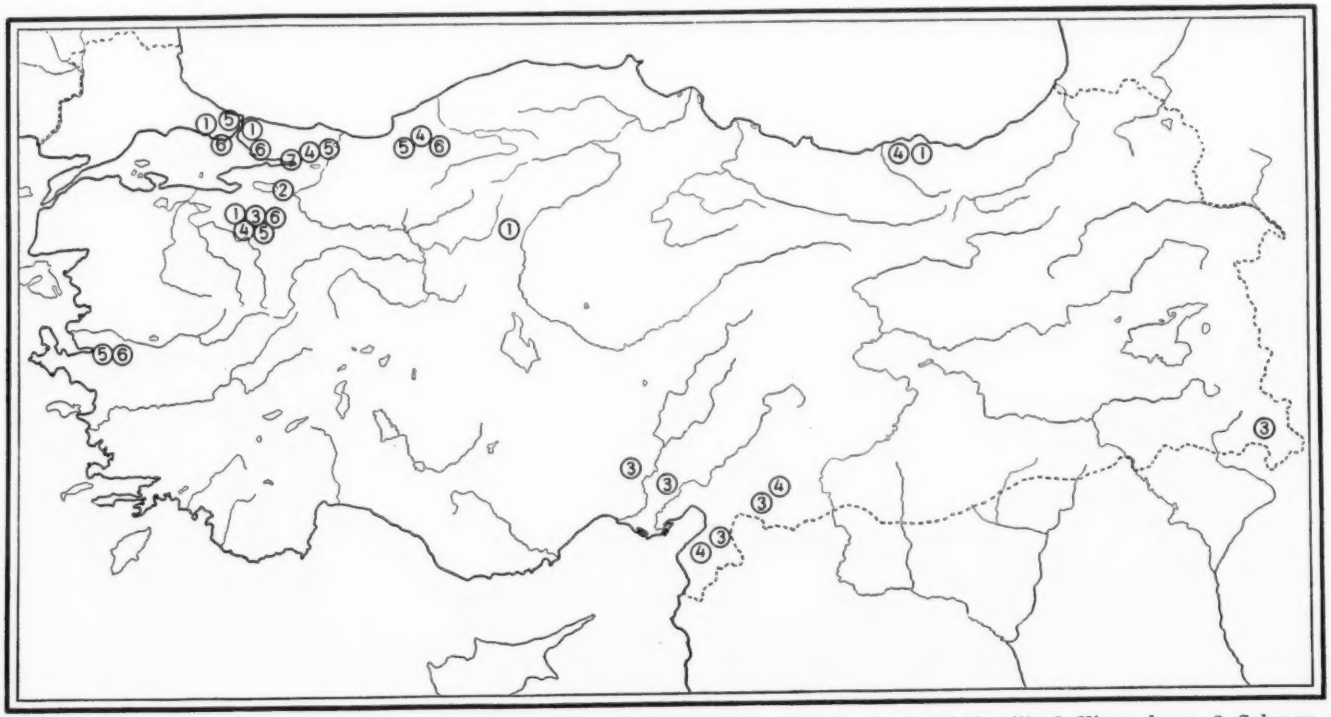

FIG. 3. Reptiles and amphibians of preferentially northern distribution in Anatolia. 1. *Anguis fragilis;* 2. *Vipera berus;* 3. *Salamandra salamandra;* 4. *Triturus vittatus;* 5. *T. cristatus (Karelini);* 6. *T. vulgaris;* 7. *Bombina bombina.*

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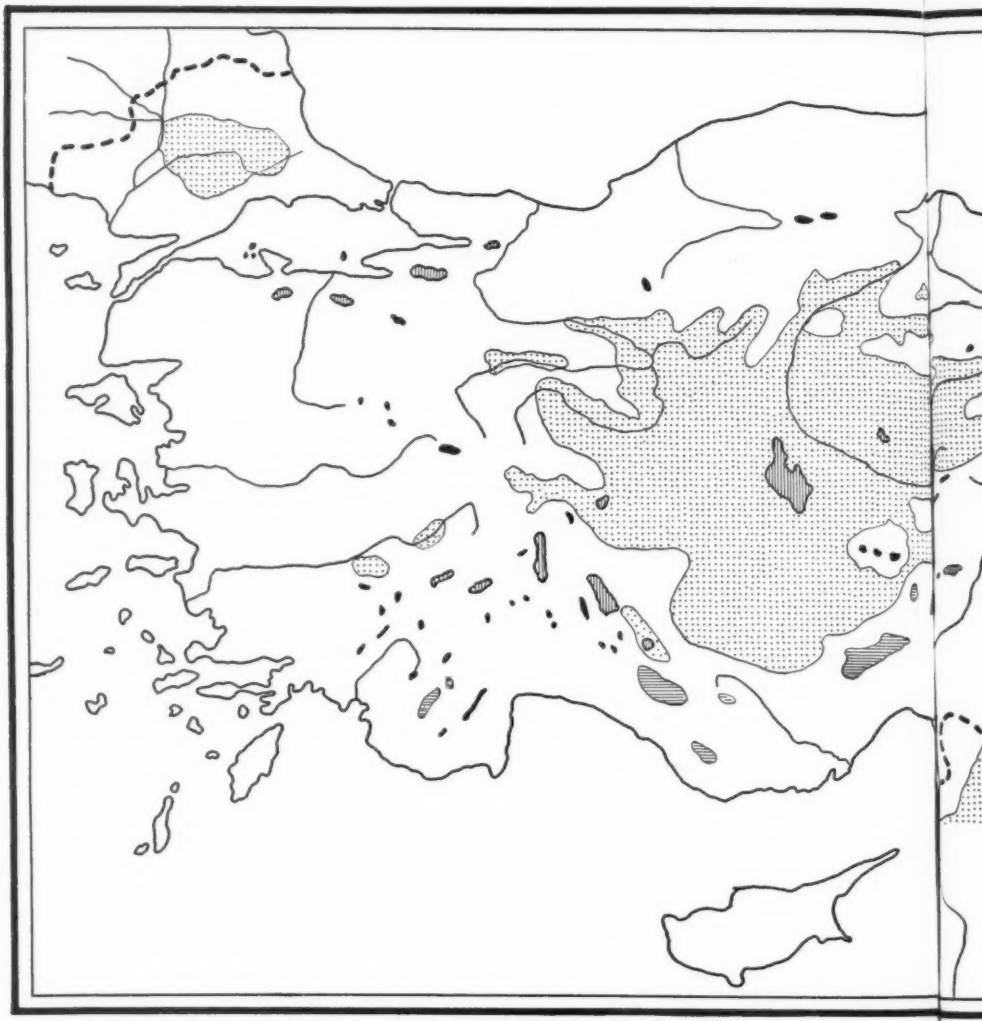
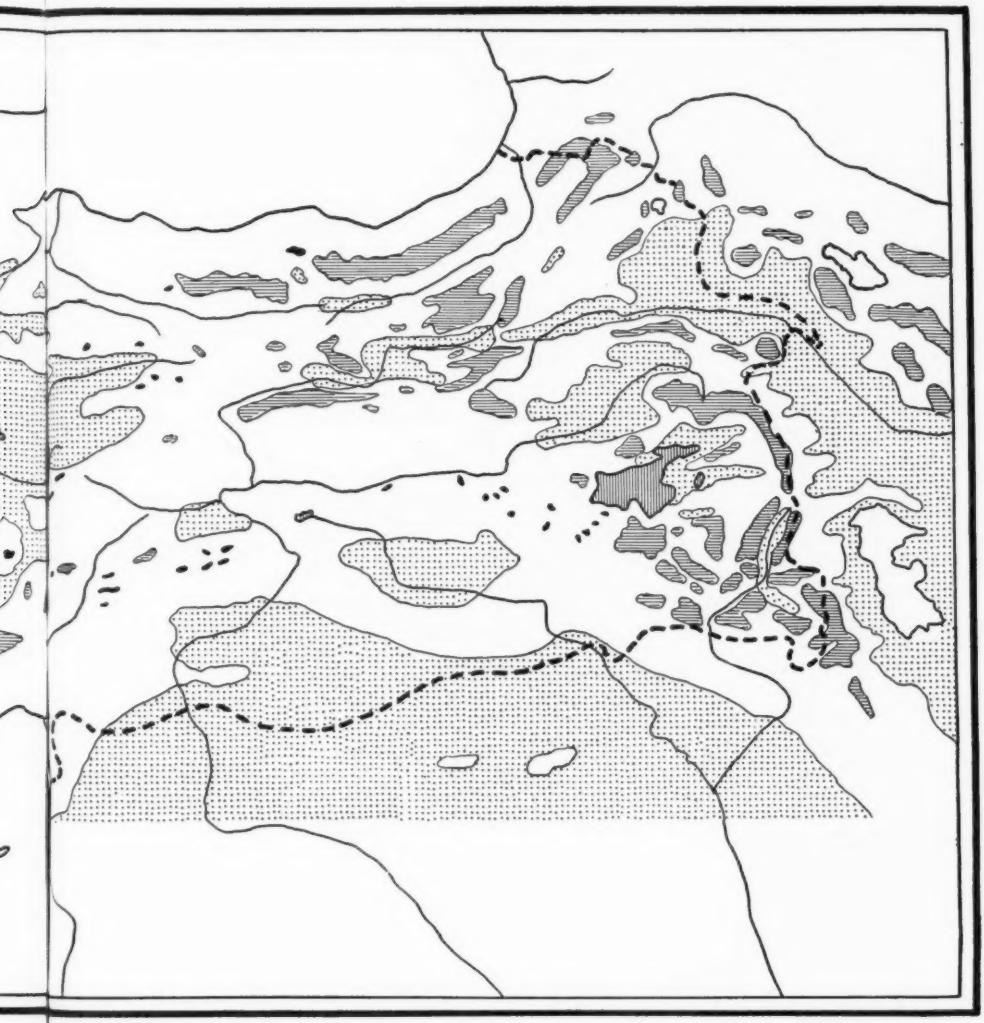


FIG. 4. The Arboreal and the Eremial in modern Anatolia. Stippled areas are steppes or large alpine zones are indicated by hatching, and small alpine areas in solid black. The re of Anatolia was originally covered by forests which persist even today in the form of sing



steppees or small groups of trees in regions where forests were destroyed by men and goats. The rforests are well developed in the northern, western, and southern mountains; those on the of singast of the Black Sea are humid, the others are dry forests. (Map drawn after Louis.)

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Relations of Anatolian Fauna

Although the Mediterranean and sub-Mediterranean element is well represented in the Anatolian millipedes and other sedentary groups, we must keep in mind that just such Anatolian species with restricted active and passive mobility have clear faunal relations, not only with the west, but also with the east of the Palaearctic, even as far as China and Japan, e.g. the genus *Amblyiulus*. Thus, it seems, we are justified in seeing in the older faunal elements of Anatolia members of a widely distributed fauna of the warmer Tertiary which once occupied a nearly continuous area in the whole Palaearctic. This fauna differentiated in the course of millions of years into forms representing one another geographically and was partly destroyed, partly driven back into refuges, as a result of the progressive climatic changes with the approach of the Quaternary.

Many land and freshwater genera of this Palaearctic fauna of the Tertiary do not exist in Siberia today, whence refuge into a more moderate climate was impossible. Anatolia offered such refuges, one in the Aegean and western Anatolian zones, the other in eastern Anatolia. These two refuges were separated from one another by high mountains in the north and in the south, and by a large freshwater lake or a system of lakes which covered an area as great as that from the sources of the Great Meander to the eastern border of Asia Minor. Although Anatolia towards the end of the Tertiary was raised up from nearly sea-level to an altitude of approximately 1000 metres, and in spite of the postglacial steppification of central Anatolia on the one hand and of the highlands around Mt. Ararat (Louis, 1939) on the other, the majority of its animals are forms of the Palaearctic Arboreal (Fig. 4). They have been settled there since the Tertiary or at least since the Quaternary. With the amelioration of the climate in postglacial times, many species of the latter group reoccupied the territories in central Europe where they were lost in the glacial period. As was mentioned above, the pumping action of the glacial period was of great importance for the mixing of northern species with the fauna of Syria, Palestine, and Africa south of the Sahara (Figs. 5, 6).

Even though the Anatolian fauna shows clear relations with that of the Palaearctic, it must be admitted that some of its species do not fit in with this rule. These forms cannot be regarded as members of a more southern fauna which arrived in southern Anatolia after the glacial epoch; it even seems very doubtful whether these forms have come into Anatolia only after the desiccation of the Syrian-Iranian Sea in the Pliocene. I should like to mention here only some examples of these old elements, which may be called Gondwanian forms. They show faunal relations between Anatolia and regions far remote in the south, these regions being separated from the major part of the Gondwana continent in such early periods as the Secondary or the beginning of the Tertiary.

Among the Anatolian millipedes the genus *Melaphe* (Attems, 1943), is to be discussed. Its area of distribution includes Albania, Thrace, Anatolia, Mauretania, and Abyssinia. The generally low mobility of millipedes and the ecological needs of *Melaphe* in particular make it improbable that the area of distribution of the genus is the result of migrations in the recent past. If we add that the most closely related genus to *Melaphe* is *Karakodesmus* in Venezuela, it sounds preferable to describe *Melaphe* as an ancient type of Gondwana origin. The same interpretation can be given to the close relationship of the blind and cavernicolous beetle *Cereaxina troglodytes* of south Anatolia (Jeannel, 1934) with the highly specialized and myrmecophilous genus *Lioclemmus* of Madagascar. The relationship of a Mediterranean and Anatolian genus of locusts, *Saga*, to genera in South Africa and Australia is an argument under the

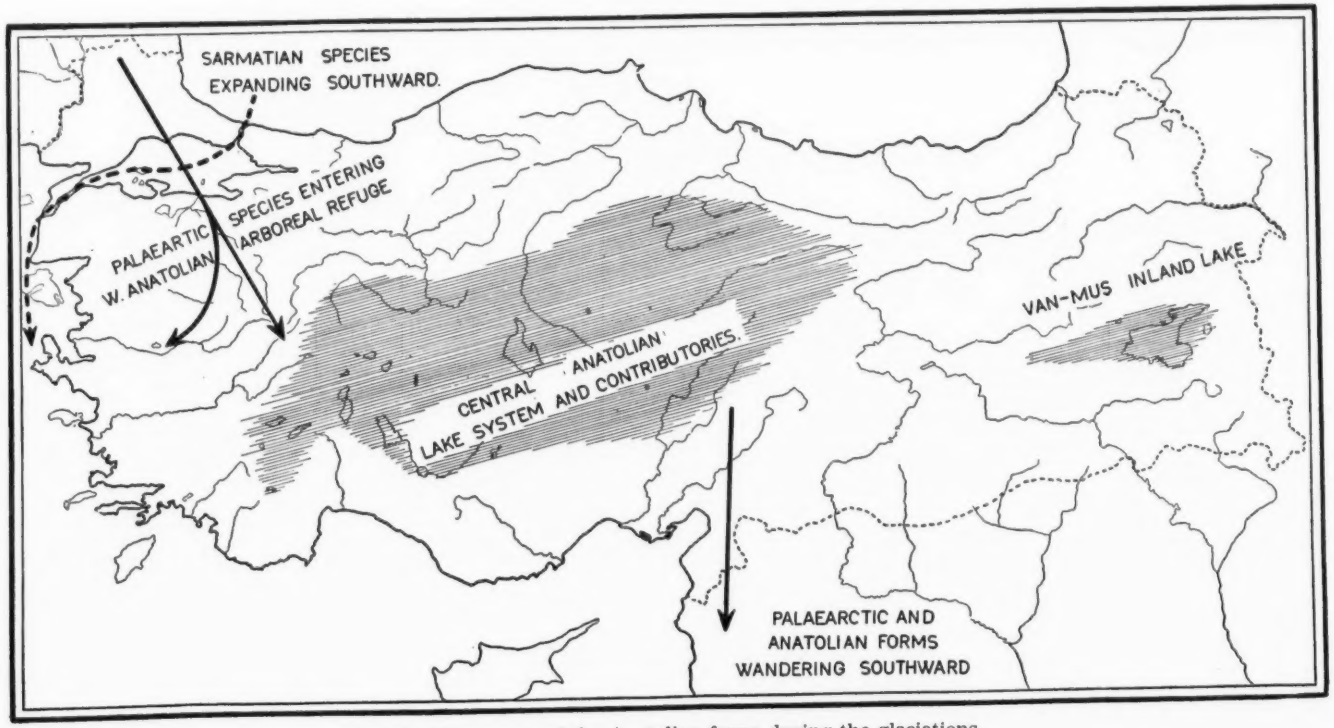

FIG. 5. Movements of the Anatolian fauna during the glaciations.

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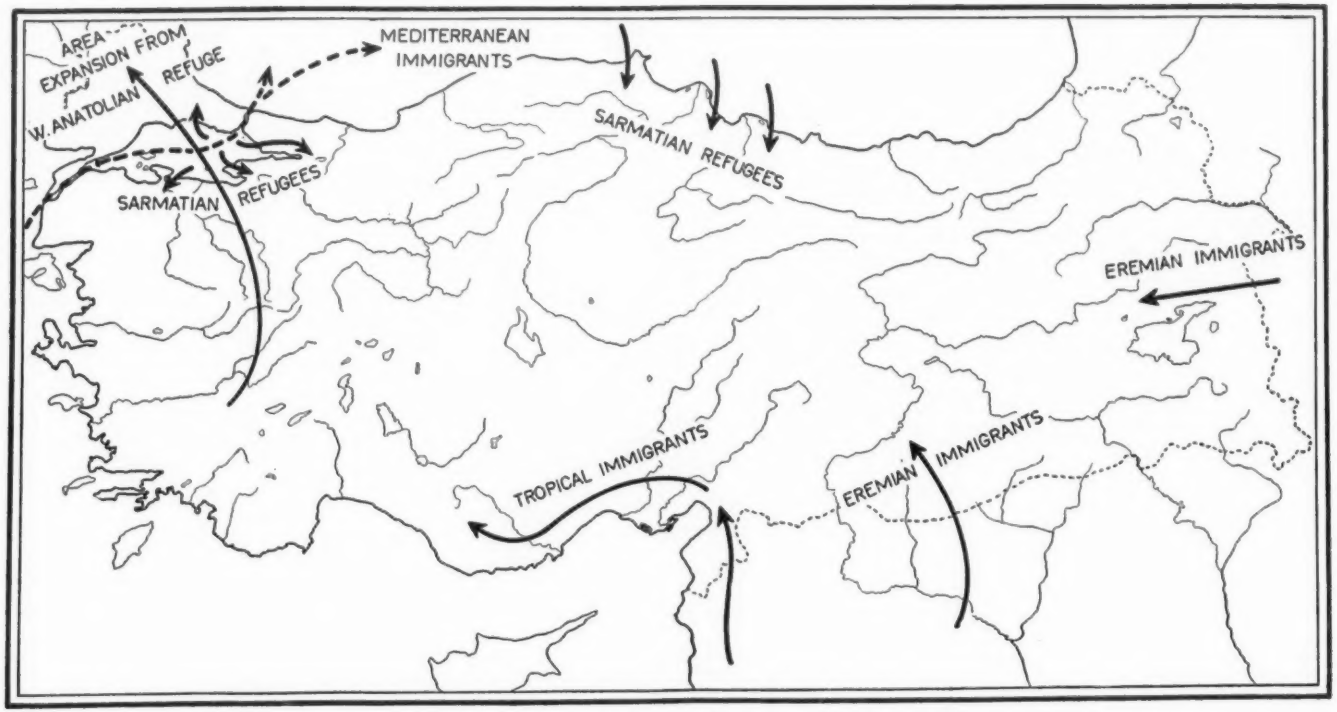

FIG. 6. Movements of the fauna in the postglacial period.

same heading. Finally, the remarkable case of the wingless earwig genus *Pseudisolabis* (Burr, 1947) may be mentioned. This genus has one species in New Zealand, which was separated from Australia in the Mesozoic, some others in Australia, Malaya, and India, and a new one recently described from western Anatolia. The presence of members of these Anatolian genera in widely removed and early separated regions of the southern hemisphere indicates the great phylogenetic age of these forms. But on account of the rareness of these examples and our deficient knowledge of geological relations in the remote past, we cannot as yet work out the history of such species in more detail.

The faunistic relations between the Far East and Anatolia can be proved by many examples from different groups of animals. They form only a small part of the very large mass of material by which the existence of a much higher uniformity of the Palaearctic fauna (and flora) during the warmer Tertiary can be shown. Contrariwise, the relations between the Nearctic and the Anatolian fauna are more or less sporadic. Nevertheless there are some highly remarkable cases by which such a relation can be shown. It has long been known that the woodlice *Mesoponorthus* are represented by one species in Middle America, and that the subgenus *Collaria* of the centipede *Scolopendra,* with many Mediterranean and one Anatolian species, has one member in Mexico. Recently another interesting case was found by Chamberlin (1952). The centipede family Gosibiidae which up to now was thought to be endemic in North America has two genera and nine species in Anatolia! (Fig. 7). The material presented as yet is not sufficient to decide by which path the distribution of these animals may have been accomplished. But it seems worth stating that the Nearctic-Anatolian relation is not indicated by cold-tolerant species which are distributed in north and east Asia and for which the use of the Bering bridge would be probable. Rather are we concerned with a relationship between animals adapted to life in the Mediterranean region and similar ones living in the Nearctic. In the case of *Mesoponorthus* a passive transport may have a low probability, but this mode of distribution seems completely improbable in the centipedes mentioned above.

Faunal Migrations

Our information is more adequate in the case of the immigrants into Anatolia from the south during the Pliocene. The best-known facts about this faunal migration are those concerning the distribution of freshwater fishes from India to Anatolia and also to Africa. The African freshwater fish fauna contains a group of forms, the characids, with clear relations to South America, besides an old and endemic element of mormyrids, bichirs, phractolaemids and others. As a result of a long divergent evolution after the early isolation of Africa from South America by the Atlantic Ocean, these elements, systematically, are considerably remote from one another. A third group of African freshwater fishes has very close systematic relationship with those of India (Kosswig, 1954*b*), for instance the genera *Barilius, Discognathus, Barbus, Clarias, Mastacembelus,* and many others. The generic identity of this third group in India and in Africa supports the hypothesis that these elements were exchanged recently, not earlier than in the Pliocene (Steinitz, 1954). There are good reasons to suppose that a more indirect route—the north Arabian-Syrian—was used for the invasion of Indian genera into Africa. This means that the tropical Indian fishes passing Syria and northern Arabia came into the neighborhood of Anatolia, which they entered freely. Some of these forms, e.g. an endemic subgenus of *Tylognathus* in western Anatolia, are still remnants of this tropical invasion from India (Figs. 8, 9.). The greater part of these Indian invaders went further to the south, leaving their traces in Palestine too. The reason

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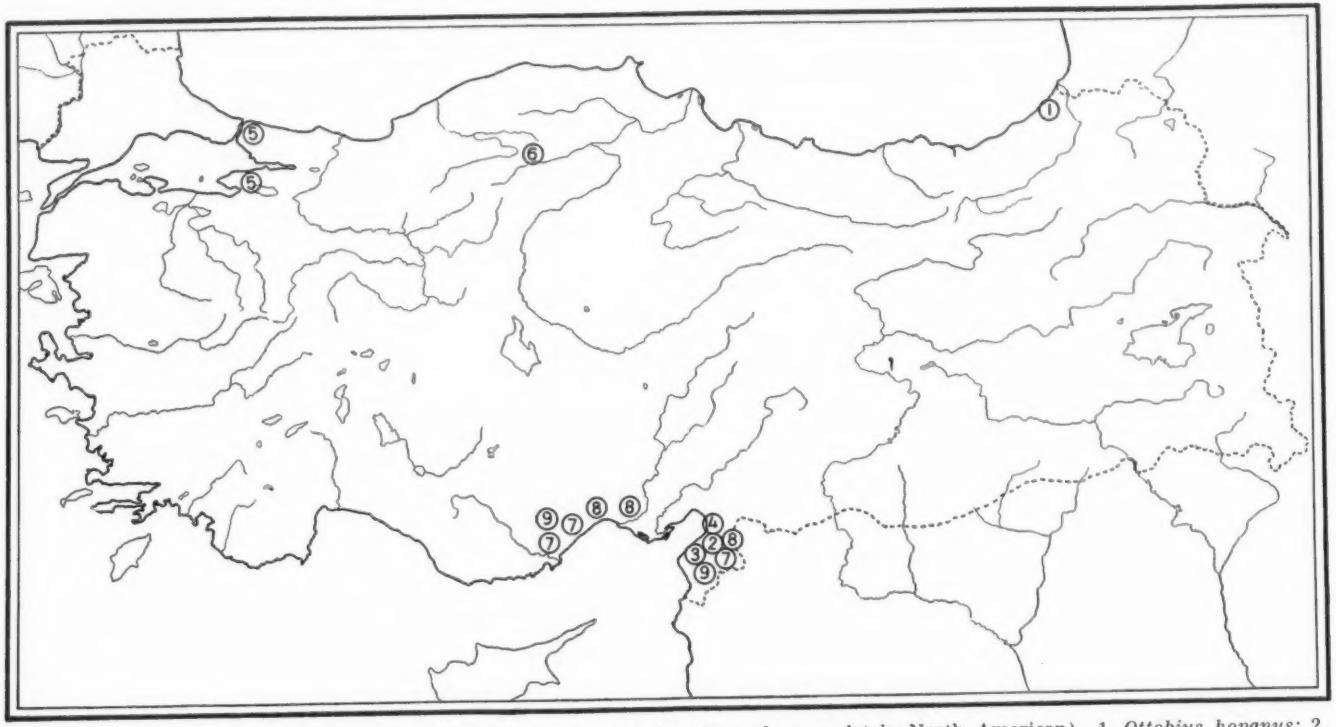

FIG. 7. Gosibiid Chilopoda in Anatolia (the family was once thought to be completely North American). 1. *Ottobius hopanus;* 2. *Turkobius adherens;* 3. *T. annexus;* 4. *T. errantus;* 5. *T. orientis;* 6. *T. plesius;* 7. *T. andrethus;* 8. *T. sogukolukus;* 9. *T. ocellatus.*

why the invasion was unilateral and why no African forms migrated in the inverse direction into India cannot be answered today. But it seems worth mentioning that such African forms as reached western Asia are also known from Palestine and Syria; this means that these forms also took the longer northern route instead of the direct route to the east where the Indian Ocean, the Persian Gulf, etc. always formed a barrier to the direct expansion of freshwater animals.

Relics of the tropical invaders from India into the Anatolian freshwater fauna are rare today. This is easily understood from the fact that at the end of the Tertiary three main factors contributed to a destruction of biotopes suitable for their existence: (1) the climatic changes in the Glacial Age; (2) the desiccation of most of the central Anatolian lakes or their transformation into azoic salt lakes; (3) the elevation of the Anatolian plains to more than 1000 metres above sea level, which resulted in very hard winters. But there are some sufficiently warm refuges, as for instance, the lakes from which the Great Meander rises, where such interesting forms still persist and now live together with other species which are of a totally different origin. In the sources of the Great Meander, swarms of a new species of *Mesomysis* (Bacescu, 1948) live together with fish of Indian (e.g. *Tylognathus Klatti*), central European (e.g. *Gobio gobio*), southern European (e.g. *Parahodeus*), and central Asiatic (e.g. *Acanthorutilus*) relationship. The crustacean mentioned above belongs to a genus the distribution of which was hitherto thought to be restricted to the basins formed by the separation of the Sarmatian Sea. This greatest inland sea of brackish to freshwater character of the second half of the Tertiary persists today in the form of three basins separated from one another: the Black Sea, the Caspian Sea, and the Aral Sea. The influence of the Sarmatian fauna on that of Anatolia was very important for relatively long periods (Kosswig, 1942; Kosswig and Battalgil, 1942). On one side the north Anatolian coast was bordered by the Sarmatian Sea, or rather, the two parts here concerned: the Euxine and the Dacian lakes. The former was saltier than the latter, and they were separated from one another by the Crimean land between the Podolian platform and Cape Bafra. As far as we can judge, the Dacian Lake was important for the faunal exchange between central Europe and Anatolia (Fig. 9). The Sarmatian Sea was joined to the Aegean lake system, which covered the territory of the modern Aegean Sea and ended in the Mediterranean near the island of Cos. The influence of central European species, the so-called Danube fauna, on the rivers Maritza, Struma, and Vardar, and in the territory of Greece and western Asia Minor, can easily be understood from this geographical circumstance (Kosswig, 1954*a*). This situation explains also the route followed by freshwater fishes of south European origin from Greece to Anatolia and vice versa. A system of rivers and lakes in the lowlands of the Aegean landmass favored the exchange of freshwater groups of animals. On the other hand, even in Tertiary or Quaternary times the Aegean lake system was a faunal barrier for animals of other ecological requirements than those of freshwater animals. For instance, the petraëic millipedes are quite different on the Asiatic and European sides of the Aegean Sea. The difference is certainly the result of a long period of isolation of the two sides by a territory the ecological make-up of which was an impassable boundary for them.

Although this interpretation seems very probable, we have to state that the presence of a number of central European and Sarmatian freshwater species or near relatives of them in Anatolia is not in accord with this assumption. The presence of *Alburnoides bipunctatus* in north Anatolian rivers flowing into the Black Sea *and* in the Euphrates, and of *Gobio gobio* in small rivers flowing into the Black Sea and also around the Great Salt Lake, are

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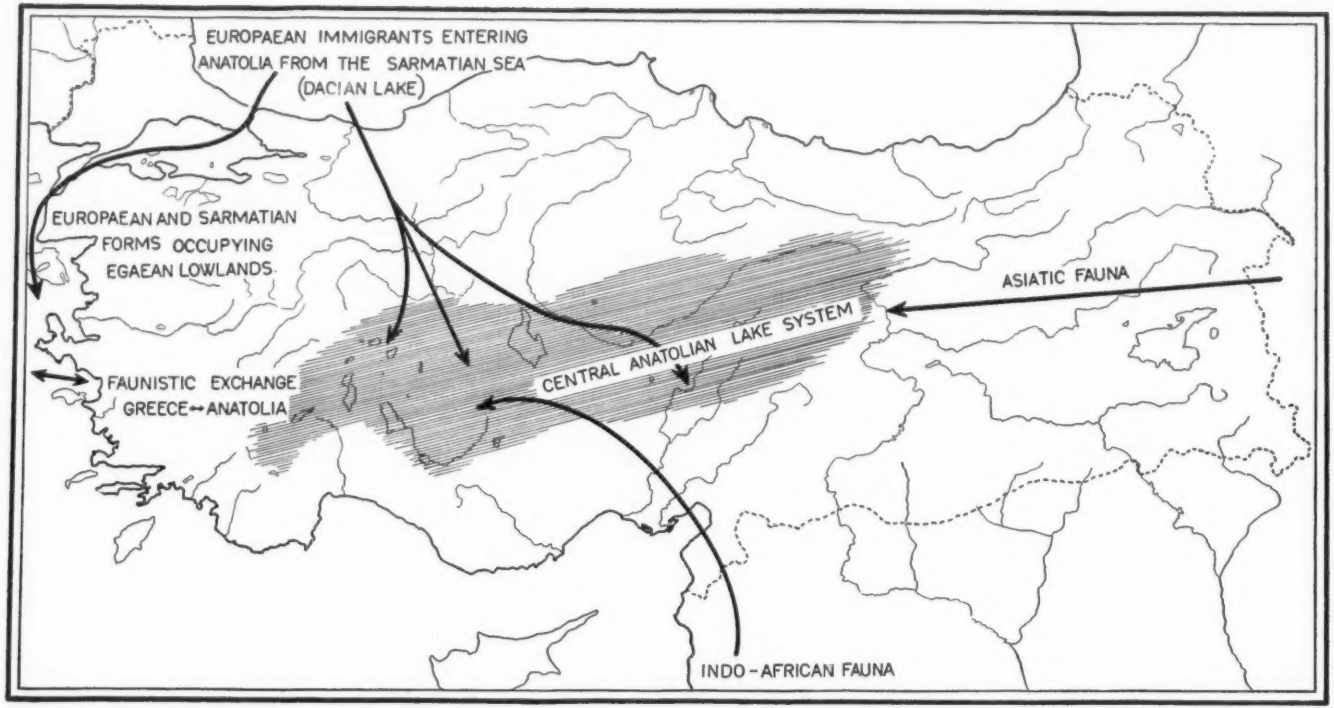

FIG. 8. Faunistic relations of the freshwater fauna in the Pliocene.

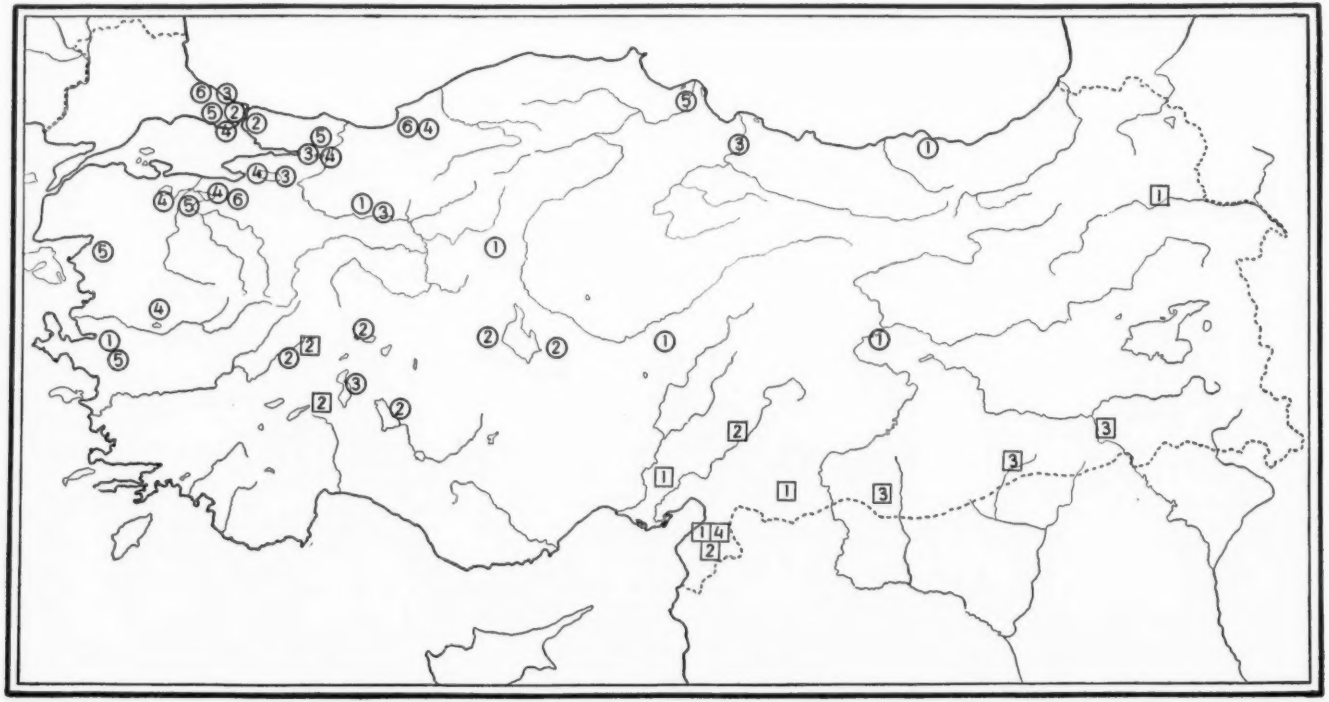

FIG. 9. Freshwater fishes of southern origin, indicated by numbers in rectangles, and fishes which are distributed also in central (eventually also in northern) Europe indicated by numbers in circles.

Southern species (in squares): 1. *Discognathus* (3 species); 2. *Tylognathus* (2 species); 3. *Mastacembelus halepensis;* 4. *Clarias lazera.*

Northern species (in circles): 1. *Alburnoides bipunctatus;* 2. *Gobio gobio;* 3. *Vimba vimba* (+*tenella*); 4. *Chalcalburnus chalcoides;* 5. *Rhodeus sericeus;* 6. *Tinca tinca.*

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facts under this heading. It is not very satisfying to regard these fishes as late invaders during the glacial period in which the invasion of elements of a more northern fauna into Anatolia was easy and actually accomplished by many species with good locomobility. The formation of a series of subpecies of *Gobio gobio* in central Anatolia and even of a closely related endemic species (*Gobio hethiticus*) indicates a longer period of stay of these elements in Anatolia. The presence of the remarkable Sarmatian genus *Mesomysis* in central Anatolia also requires another interpretation. It is quite impossible to assume that these small mysids which live in lakes wandered actively against the currents of rivers coming from the Anatolian high plateau and sending their waters into the glacial Black Sea. It is more probable that the genus arrived early, at a period when there was no great difference between the altitude of Anatolia and the sea level. Under these conditions a lake-dwelling species could actively extend its range. Such a situation can be imagined only in the Pliocene or earlier, i.e. in a period when the Asiatic freshwater fauna, especially the Indian forms, had just begun to enter Anatolia. We can therefore suppose that central European and Sarmatian species of the north Anatolia coast spread southwards by two routes: The one was via the Northern Marmara basin and the Aegean lowlands, a route which existed for a long time; it was restituted during each glaciation and interrupted during the interglacials when the Mediterranean covered this region, extending as far as the Black Sea. The other route lay further to the east, and it is by this route that Anatolia could be reached (Fig. 8).

After the breakdown of the Aegean continent in glacial times, the faunal exchange between Greece and Asia Minor ceased. By the newly formed Aegean Sea many species extended northwards from the Mediterranean into the Sea of Marmara and the Black Sea, which were at this time separated from the Caspian; in the Caspian the old Sarmatian fauna of brackish or fresh water has been able to persist up to the present, whereas in the Black Sea this Sarmatian element was partly destroyed and partly driven into the deltas of its great rivers or into lakes separated from the basin of the Black Sea itself. More than 75 per cent of the fish species of the Black Sea today are of Mediterranean origin (Slasdenenko, 1936). A number of species return for spawning into the Sea of Marmara (e.g. the mackerel, *Scomber scomber*) or even into the Mediterranean (e.g. the tunny, *Thunnus thynnus*) after having visited the rich feeding grounds of the Black Sea. The economic importance of the Bosphorus depends essentially upon the intensive fishing provided by the regularly migrating species, such as mackerel, bonito, and others.

Some species have adapted themselves completely to the conditions in the Black Sea and can in part be distinguished from their Mediterranean congeners (e.g. the anchovy, *Engraulis encrasicholus;* the gar pike *Belone belone*, and others). The bonito (Nümann, 1953) shows extraordinary migratory behavior. Both young and old migrate south out of the Black Sea, and many of the younger individuals seem not to return. The older ones leave the Sea of Marmara in summer for the Black Sea without having spawned. The old homeland with its higher salt concentration is no longer the spawning place but merely a region into which a part of the Black Sea population wanders for the winter. The reason for this peculiar behavior is not known as yet.

Besides the tropical forms of Indian origin in the Anatolian fauna of freshwater fish, there is one other group of fishes which is completely lacking in Europe. For this the cyprinid genera *Acanthorutilus* (Anatolia and Mongolia), *Varicorhinus*, Anatolia, Transcaucasia, Syria, Palestine, Africa), *Acanthobrama* (western Anatolia to Palestine, its nearest relative *Capoëtobrama* in the Amu Daria and Syr Daria in central Asia), and *Schizo-*

FIG. 10. Fishes of central Asiatic relationship in Anatolia. 1. *Schizothorax prophylax;* 2. *Acanthorutilus* (3 or more species); 3. *Acanthobrama* (3 species).

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thorax (central Asia and as a glacial relic in India) can be named. The Bosphorus is, from the geological point of view, a very recent formation (Pfannenstiel, 1944); nevertheless it is an absolute barrier to the westerly distribution of all these Asiatic forms (Figs. 10, 11). The rich representation of some of these genera in Asia Minor and the distribution of some of their species over many river systems of Anatolia favor the assumption that the relative age of these forms is great. If this statement is correct, the original western frontier of all these species cannot have been the Bosphorus and the Aegean Sea, only formed, as seen above, during the Quaternary. It is more probable that these forms, which are richly represented in the mountainous regions of western and central Asia, entered Anatolia so early that they could make full use of the way southward into Palestine and even into Africa. This way is known as the Pliocene land-bridge in the Syrian-Iranian area. If this hypothesis is true, the Bosphorus and the Aegean Sea could not play the decisive role in the separation of these Asiatic genera from Europe. The frontier of these Asiatic elements in Anatolia was more likely the western Anatolian mountain system, by which the Aegean zone is separated from the plains of central Anatolia (Fig. 12). It is a well-known fact that the upper beds of the different rivers on the Aegean slope of the western Anatolian mountains have retained only secondary relationship with the central Anatolian high plateau and the remnants of the lake system which once covered it. The overground connection of these lakes is even now only partially extant; many lakes send their waters by underground passages through the mountains to the rivers on the Mediterranean or the Aegean slopes of southern and western Anatolia.

Similarly, in the south and in the north, high mountains separated the central Anatolian lake from the Mediterranean as well as from the Black Sea (i.e. the Sarmatian coast). From the east, on the other hand, the entrance into central Anatolia was more or less open and facilitated by the upper reaches of the eastern Anatolian rivers, which flow from east to west. The union of the Aegean coast with central Anatolia by the modern river systems was definitely effected after the Aegean continent broke down. As the Asiatic forms came too late, they found no freshwater routes by which to pass to the European side of the Aegean Sea.

Let us now return to the problems concerning the Anatolian steppes. As stated above, the altitude of Anatolia was reached only in the course of the second half of the Tertiary or even later. Salomon-Calvi (1939) dates the rise of Anatolia as late as in the Quaternary, supposing that the two phenomena, the Aegean subsidence and the elevation of Anatolia, were the expression of the same crustal movement in this region. The Tertiary climate in the interior of Anatolia was warmer and wetter than it is today. In the Quaternary the humidity increased. As a result, the surface of the lakes which have persisted to the present day as brackish water, like the lake of Burdur, at that time stood 90 metres higher (Louis, 1938). Remnants of old lake terraces with clearly visible traces of the eroding waves surround the Great Salt Lake; the lake of Van is only a small relic of a greater inland sea, covering not only the territory of the lake of Van but also that of the plains of Mush. The majority of the central Anatolian lakes were in connection with one another (Lahn, 1948). A rich vegetation surrounded this watered panorama of glacial Anatolia.

Recent research has shown that the natural lower boundary of forests of a more or less dry type lies so deep that even today the whole area from the west of Malatya to Bitlis must be included in the forest zone and does not belong to the steppe facies (Louis, 1939). Natural steppes are found in central Anatolia, in the high plateaux around Mount Ararat, and in the south of the eastern Toros, in

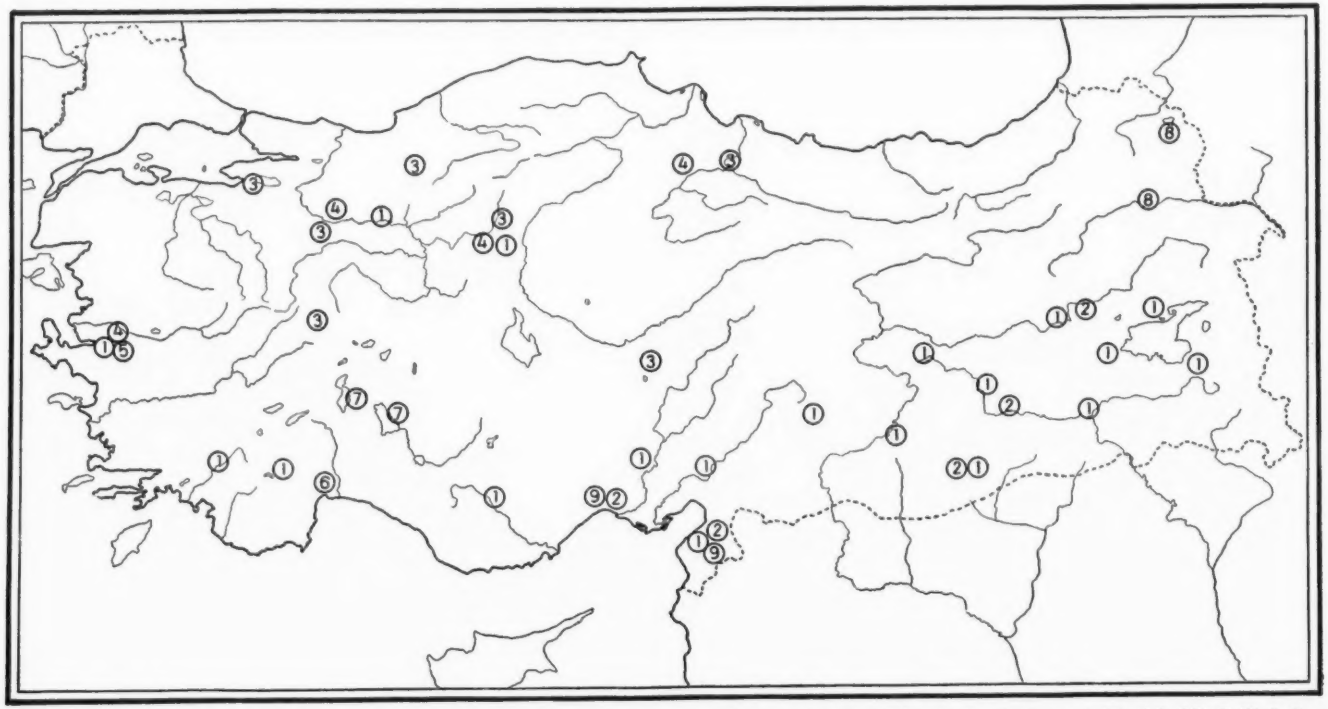

FIG. 11. The distribution of the genus *Varicorhinus* in Anatolia. 1. *V. damascinus;* 2. *V. trutta;* 3. *V. tinca;* 4. *V. sieboldi;* 5. *V. holmwoodi;* 6. *V. antalyensis;* 7. *V. pestai;* 8. *V. capoeta;* 9. *V. barroisi.*

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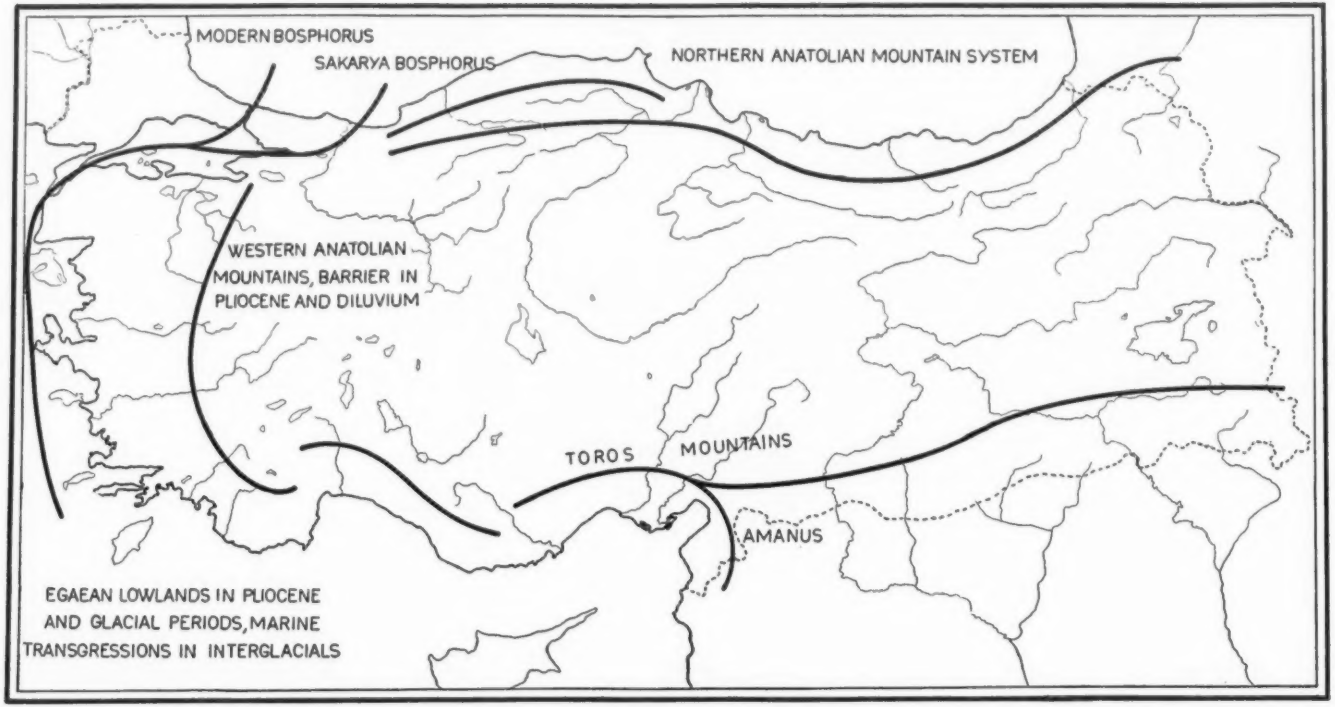
MODERN BOSPHORUS
SAKARYA BOSPHORUS
NORTHERN ANATOLIAN MOUNTAIN SYSTEM
WESTERN ANATOLIAN MOUNTAINS, BARRIER IN PLIOCENE AND DILUVIUM
TOROS MOUNTAINS
AMANUS
EGAEAN LOWLANDS IN PLIOCENE AND GLACIAL PERIODS, MARINE TRANSGRESSIONS IN INTERGLACIALS

FIG. 12. Barriers to the distribution of species. In addition to the mountain systems in northern, southern, and western Anatolia, the Aegean lowlands acted as a faunistic barrier, either as a system of fresh or brackish water in glacial periods and in the Pliocene, or as the result of a marine transgression. Before the functioning of the modern Bosphorus there was a communication in interglacial periods between the Black Sea and the Mediterranean through the Sakarya Bosphorus of Pfannenstiel.

the area which forms the continuation of the warmer Syrian steppes towards the north. The fauna of these Eremial regions is derived to a great extent from forms which in earlier times inhabited the Arboreal, but still exist in the same regions which underwent steppification later. The Anatolian butterflies and moths, for example, have systematic relationship mostly with the central European and Mediterranean fauna, but not with that of central Asia, where, for a very long period, the Eremial facies has been characteristic. Among the mammals of Anatolia, especially in the rodents, the percentage of steppicolous species is greater than in most other orders. *Spalax, Spermophilus, Alactaga, Cricetulus* may be mentioned here. In the Reptilia the number of typical Eremial genera is high only in the eastern steppe zone, i.e., the Ararat plateau. Here *Phrynocephalus, Eremias,* and *Eumeces* represent the real Eremial fauna. Only one species, *Eumeces schneideri,* has been found once in the well-investigated central steppes near Ankara. In this latter region, besides the euryoecious *Ophiops elegans,* a species of *Lacerta, Lacerta parva,* derived from the Arboreal, has adapted itself to the conditions of life in the steppe. The same is true for the remarkable, rare, and primitive *Lacerta princeps* in the southern Anatolian steppes (Mertens, 1952). (Fig. 13.)

The Marine Fauna

Even in a short review of only some of the problems of historical zoogeography in the Near East, the marine fauna with its changing scenery cannot be neglected. In the beginning of the Tertiary, the Tethys Sea covered large areas which today are dry land. From the West Indies to the Pacific Ocean a rich community of tropical animals populated the littoral zone of this sea, surrounded by coral reefs. In the second half of the Tertiary great changes occurred in that part of the Tethys which was finally to be transformed into the Mediterranean of today. Landbridges rose, cutting off the continuity of the sea. The loss of communication with the Indo-Pacific has lasted to the present. The rich fossil-bearing beds of Lebanon and of Monte Bolca in Italy give us information about the great number of tropical genera in the Mediterranean of that time, while now they are confined to the Indian and Pacific Oceans. Ekman (1935) found general agreement for his thesis that the extinction of the tropical fauna of the Tethys in the Mediterranean was the result of the fall in temperature in late Tertiary and Quaternary times.

In the modern fauna of the Mediterranean, again, tropical forms play the decisive role, but these forms are related mainly to the fauna of the warmer parts of the Atlantic Ocean. Besides these, species with boreal relationship can also be found. It is probable that they entered the Mediterranean in the recent past, when, as a result of the cooling of the Atlantic to lower latitudes, the boreal area extended further to the south. Some of the boreal invaders of that time persisted in the Mediterranean into the postglacial period, mixing with aggressive and euryoecious species of tropical and subtropical distribution in the Atlantic. It is still not known definitely whether the majority of these species persisted in the Mediterranean itself during the period of its separation into different parts and its cooling or—as is more probable—whether they later reoccupied this sea. The ecological efficiency of these species is clearly demonstrated by the fact that they freely entered the much colder Black Sea, definitely establishing themselves there. As a result of the rhythmic transgressions of warmer Atlantic waters to the north, truly equatorial species of this ocean appear from time to time on the English coast and more frequently in the Mediterranean, especially in its western parts and on the Algerian coast. But such forms apparently are not sufficiently adapted to the conditions in the Mediterranean. Some which persisted remain

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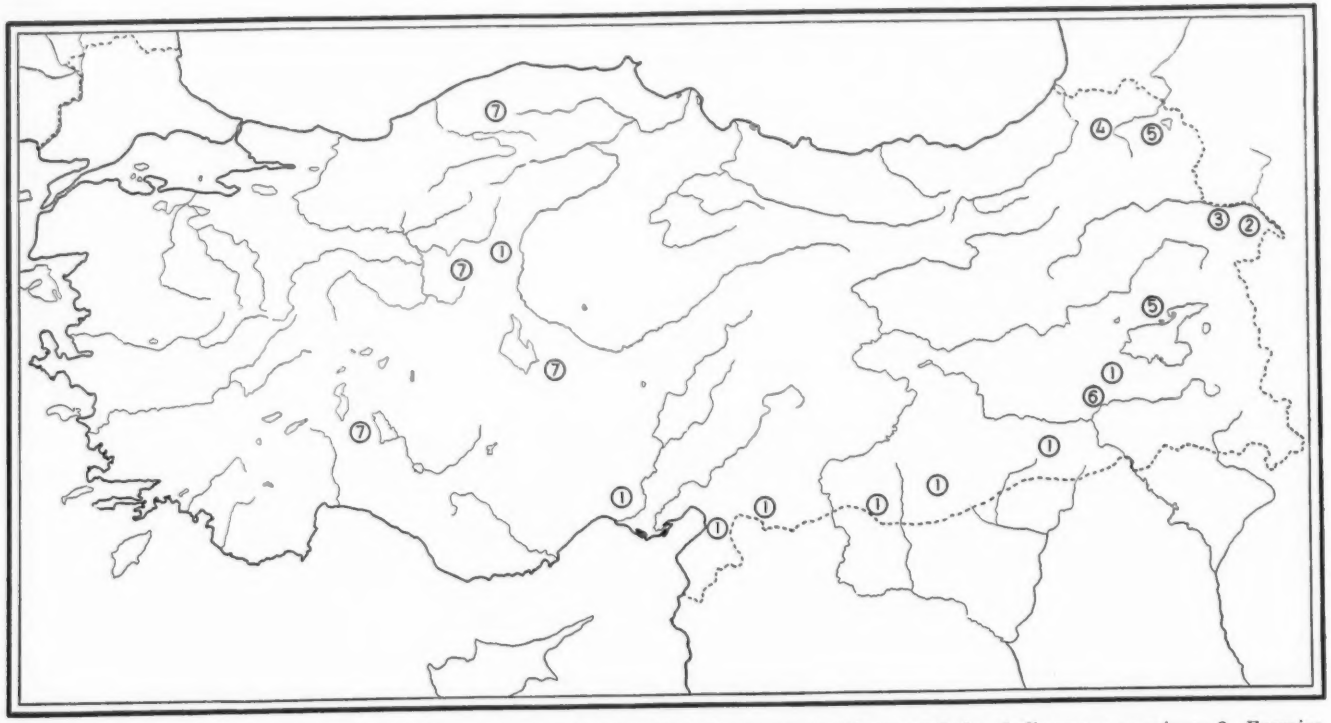

FIG. 13. Steppicolous lizards of Anatolia. 1. *Eumeces schneideri* (2 races); 2. *Phrynocephalus helioscopus persicus;* 3. *Eremias pleskei;* 4. *Eremias arguta;* 5. *Eremias velox strauchi;* 6. *Lacerta princeps;* 7. *Lacerta parva.*

rare, others died out after short periods, e.g. *Diodon hystrix*.

It is not certain whether for this phenomenon physical or biological conditions are decisive. For instance, the prior occupation of all ecological niches by well-adapted species could have prevented the successful establishment of these late invaders from the equatorial regions of the Atlantic. Information, for which we are indebted to W. Steinitz (1927, 1929), is sufficient to contradict this view. Since the opening of the Suez Canal in 1869 an invasion of the Mediterranean by species of the Indo-West Pacific fauna has begun. These species coming from the Red Sea, the warmest and saltiest sea we know, have passed through the Suez Canal with its changing and extreme ecological conditions, probably in the course of some generations, and safely reached the Mediterranean. Ten species, which have expanded into the eastern Mediterranean by the aid of the northward current, were recorded by W. Steinitz from Haifa in 1927. Another ten were added to this list twenty years later by G. Haas and H. Steinitz (1947). Ben-Tuvia (1953) described the presence of eight other species which arrived in the Mediterranean off the coast of Israel. Ten species at least, partly different from those known from Haifa, can be found in Alexandretta (Kosswig, 1950); four of them are known from Rhodes at the entrance to the Aegean Sea, since 1943. All these facts indicate that these tropical Indo-Pacific forms, with very different biological requirements, have found a great variety of suitable ecological niches. The degree of plasticity which these Erythraean fish, Crustacea, bivalves and others show, is remarkable and not in harmony with Ekman's supposition that the ancestors of these new invaders died out in the Mediterranean at the end of the Tertiary as a result of the cessation of the limited environment in a tropical coral sea.

The animals of the tropical Tethys Sea had millions of years at their disposal for their adaptation to the cooling of the climate in the Tertiary. We must conclude that at least conditions such as those prevailing today in the southern Aegean Sea are well within the range of tolerance of those Erythraean animals which at present are flourishing there and expanding their area of distribution, e.g. the fishes *Mulloidichthys auriflamma* and *Siganus rivuletus* and the crab *Portunus pelagicus* (Fig. 14). It therefore seems more probable that the dying out of the tropical Tethys fauna is merely the result of either a further lowering of temperature or a change in salinity in the Mediterranean during the glacial periods when Arctic species (*Cyprina islandica, Plautus impennis*) lived in that sea.

This invasion of Erythraean species into the Mediterranean is the more remarkable as reverse infiltration of Mediterranean forms into the Red Sea has been very limited (Gohar, 1954). Among the fishes of economic importance, only *Serranus cabrilla* and *Sciaena aquila* may be mentioned; these are frequently caught in the Red Sea as far as 90 km. to the south of Suez. Although the Red Sea itself represents a relatively young geological structure, it seems that at the moment of its formation species adapted to all ecological niches were waiting *ante portas* to enter this sea. In the Mediterranean the situation is quite different. It is possible that there are, even now, free ecological niches in the eastern Mediterranean although approximately 80,000 years have passed since the last culmination of the glacial period (Würm I), and some 18,000 years have passed since the last, but less important, glaciation (Würm III). Or it may be that the Atlantic species, the older inhabitants of the eastern Mediterranean, are less adapted to the conditions in this sea than are the newcomers from the south.

These invasion phenomena correspond in an interesting way to the ingress of Mediterranean species into the Black Sea at the end of the glacial period, also against a gradient of temperature and salinity. Here zoogeographical phenom-

FIG. 14. Erythraean species off the Anatolian coast. Fishes: 1. *Stephanolepis ocheticus;* 2. *Mulloidichthys auriflamma;* 3. *Siganus rivulatus;* 4. *Atherina pinguis;* 5. *Leiognathus klunzingeri;* 6. *Holocentrum rubrum;* 7. *Tetraodon spadiceus;* 8. *Upeneus* cf. *tragula.* Crustacea: 9. *Portunus pelagicus.*

ena touch on problems of genetics and evolution, the discussion of which is outside the scope of this paper. It may be sufficient to consider briefly the results of the greatest biological experiment man has ever undertaken, albeit unwittingly: the opening of the Suez Canal. The ensuing ingress of species from the Red Sea into the Mediterranean cannot be understood as adaptation resulting from slow and stepwise genetic changes, but only as the sudden manifestation of ecological potentialities which for many generations had never been tried and which could never have been of functional significance. The same may be true for the occupation of the Black Sea by warmth-loving newcomers from the postglacial Mediterranean, when communication between the two seas was established by enormous geological changes which occurred in a relatively very short period of time.

As stated above, it is not clear to what degree modern Mediterranean species have persisted in that sea in the second half of the Tertiary and in the Quaternary. The temperature underwent extensive fluctuations, allowing the invasion of boreal and Arctic forms at one extreme and of tropical species such as *Strombus bubonius* and *Purpura haemo-*

stoma at the other. The sea level also fluctuated during the glacial periods, being lowest during the glaciation when large quantities of water were bound as ice near the poles. The Mediterranean at such times of lowest level was transformed into an inland sea and partially, if not completely, divided into two parts by the exposed land connection between Sicily and North Africa. H. Steinitz (1949) is inclined to suppose that the modern Mediterranean blennies are relics *in loco* of the Tethys in our region. But it must be kept in mind that, like most marine animals, blennies have pelagic larvae, which by passive locomotion could re-occupy an area lost in the past.

On the other hand there are, in fact, relics of the old fauna of the Tethys even in places where they would be least expected to survive: in fresh and brackish waters of the Anatolian plateau, as well as in similar biotopes in the regions around the Mediterranean which are nearly at sea level. I should like to draw attention to a family of small fish, the cyprinodontids. The genera *Cyprinodon* and *Aphanius* consist of some species in central and southern North America, and others around the Mediterranean and in central Anatolia, in the Dead Sea region, and finally in the western part of the Indian Ocean, including the Red Sea. Apparently this distribution as a whole corresponds to the western part of the Tethys. Everywhere these small fish live in such biotopes as marine coastal waters, the mouths of rivers, in lakes in the neighborhood of the sea, in fresh and salt springs inland, swimming freely in waters of very different salt concentration. As stated above, Anatolia, nearly at sea level in earlier geological periods, was elevated later. Cyprinodontids, having migrated inland, were thrust up with the rising Anatolian land mass. Because of their euryhalinity, they were able to survive in many places and today form one of the most characteristic groups in Anatolia and also in Palestine. It may be added that the enormous degree of variability with which we are confronted in the Anatolian cyprinodontids seems to be caused by interspecific or even intergeneric crosses in the past (Aksiray, 1952). Many of the populations of these fishes which at first sight look like different species, subspecies, or even genera are in reality, as it seems, nothing other than groups of a large hybrid swarm which in isolated populations have attained a more or less clear degree of uniformity; other populations are still heterozygous and composed of many different phenotypes.

It is probable that other survivors (Kosswig, 1943; Lohmander, 1939) of the Tethys are to be found among some of the subterranean genera of invertebrates around the Mediterranean and in Central America, including relatives of many marine forms of today. Such genera as *Caecosphaeroma, Monolistra,* and others may be mentioned. The transition of the ancestors of these cavernicolous forms to life in darkness was most probably accomplished by adaptation to specialized conditions of life in dark, cave-like places in the sea. Later, by the elevation of such formations rich in limestone, these forms became members of the subterranean inland fauna, without having passed through a stage of phylogenetic development in the superficial freshwaters of the continents.

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A Portable Lighting Fixture for Record Photography

HUGO G. RODECK

ABOUT two years ago it became necessary to develop a technique for the photography of the painted designs in a large number of prehistoric pottery bowls, as a record of the zoomorphic and anthropomorphic pictures painted on the inner surface. The specimens were to be studied and photographed in museums, galleries, dealers' stocks, and private collections from Massachusetts to California, and from Wisconsin and Michigan to Texas. It was anticipated that the photographs would have to be made under all manner of physical conditions and lighting facilities. Since the usefulness of the records would depend to a considerable extent on their uniformity, it was decided to develop a fixture which could be packed and transported easily by automobile and which could provide complete uniformity of photographic lighting.

Because of the special problem of uniform illumination all over the concave interiors of the vessels, it appeared that it might be desirable to adapt one of the circular fluorescent tubes in such a way as to permit the camera to see through the center of the circle. In this manner the rays from the circular lamp could cross in front of the lens and illuminate the complete interior, to the very rim, at an advantageous angle, with no tendency for the bowl rim to cast shadows.

Preliminary sketches were made, and with the cooperation of a sheet-metal worker and an electrician, the device here illustrated was perfected (Fig. 1). It was used with an Exakta 35 mm. camera with Penta Prism view finder and 50 mm. lens, the whole camera-illuminator combination mounted on a Quick-Set Junior tripod as shown. With its aid, some 3500 photographs were made in 88 different collections over a period of 4½ months, in basements, attics, exhibit halls, offices, sheds, stores, and private homes. Except for two occasions when it was burned out by being inadvertently plugged into direct current, it performed uniformly and without failure. When burned out, it was easily repaired by purchasing the standard ballast and fluorescent tube which went into its construction.

Photographs made with this lamp were uniform in nearly every respect. Exposure time was calculated by the use of an electronic exposure meter. The only serious lack of uniformity in the photographs resulted from forgetfully moving the whole mechanism in close for close-ups without reducing the exposure time to make up for the increase in illumination.

Essentially, the device utilizes a 32-watt Circline fluorescent tube in a specially built angel-food-cake-pan type of reflector, with a bracket to hold the camera so that it looks through the center of the circle. Most of the electrical appurtenances are attached to the back of the reflector except for the heavy ballast, for which a special metal case was constructed to lie on the floor and thus avoid the hazardous top-heaviness which would have resulted from mounting the heavy ballast on the tripod with the reflector and camera. A standard plug and cord connects the ballast to a source of 110–120-volt alternating current. The lamp itself plugs into an outlet in the ballast case, and in order to prevent any inadvertent direct connection of the unballasted lamp to the 110-volt A.C., a 3-way plug and socket was employed here, one

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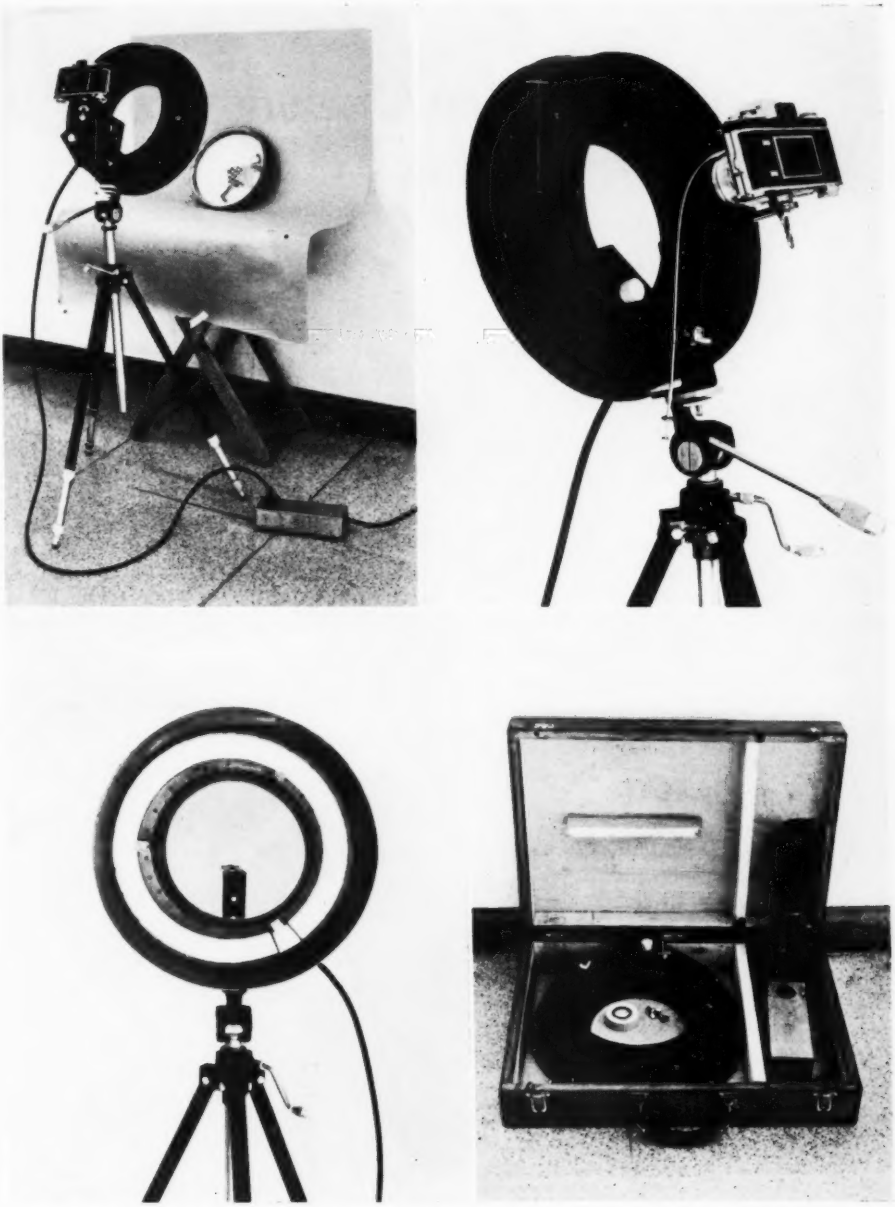

FIG. 1. *Upper left.* Portable fluorescent lighting fixture, as employed in the photography of designs on the interiors of prehistoric pottery bowls. Note the heavy electrical ballast in metal box on the floor.

Upper right. Close-up of rear of fluorescent lighting fixture, showing camera mounted in axis of circular reflector. Slotted camera bracket permits camera to be advanced without moving reflector.

Lower left. Front view of circular fluorescent fixture, showing 32-watt tube in metal reflector.

Lower right. Carrying case designed to hold circular fluorescent lighting fixture, including camera bracket, ballast case, and an extra-long extension cord.

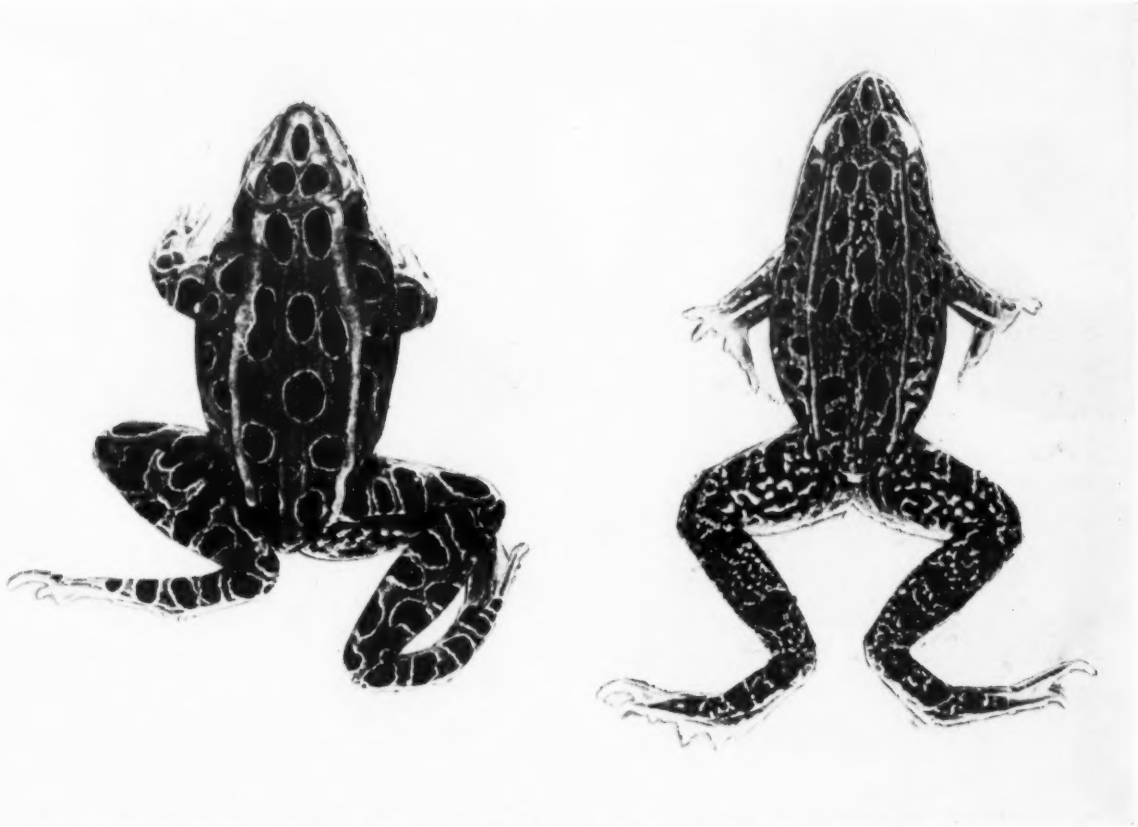

FIG. 1. *Rana pipiens* (left) and "*Rana kandiyohi*" (right) from Minnesota. These were the females used in Experiment C.

A Taxo-genetic Analysis of the Status of *Rana kandiyohi* Weed

E. PETER VOLPE

COLLECTIONS of the common leopard frog, *Rana pipiens*, from Minnesota contain occasional individuals that display a unique color pattern. These exceptional individuals exhibit the black spots characteristic of the common leopard frogs, but are distinguished by vermiculate mottlings in the interspaces between the black spots (Fig. 1). The "mottled" leopard frogs have been reported (Weed, 1922; Swanson, 1935; Breckenridge, 1944; Wright and Wright, 1949) to inhabit the southwest quarter of Minnesota, and to coexist in this limited range with *Rana pipiens* (Fig. 2).

The herpetological literature contains a diversity of opinion as to the relationship of the mottled leopard frogs to the common leopard frogs. In 1922 Weed, impressed by the distinctive pattern of the mottled leopard frogs, delimited these forms as a separate species. Weed's taxonomic designation of the mottled leopard frogs has not been universally accepted. Kellogg (1932), Stejneger and Barbour (1939), and Breckenridge (1944), among others, have not recognized *Rana kandiyohi*. Wright and Wright (1949) have listed the mottled leopard frogs as a subspecies of *Rana pipiens*. Schmidt (1953), in his *Check List of North American Amphibians and Reptiles*, has dismissed *Rana kandiyohi* "as obviously based on mutations, not at all established as subspecies." It is apparent that experimental evidence was needed before a definite statement could be made regarding the exact taxonomic status of the mottled leopard frog.

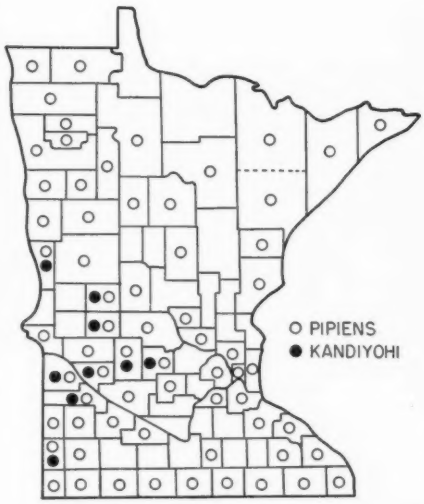

FIG. 2. Distribution of *Rana pipiens* and *"Rana kandiyohi"* in Minnesota. The distribution marks signify that the species has been found in the county indicated. Distribution map adopted from Breckenridge (1944).

Following the meeting of the A.I.B.S. at Madison, Wisconsin, September 1953, the writer had occasion to visit the Steinhilber Frog Farm in Oshkosh, Wisconsin. This provided the opportunity to compare live mottled leopard frogs with the common leopard frogs. Thirty-five mottled leopard frogs were examined and found to resemble *Rana pipiens* in every external feature except for a striking difference in color pattern. The black spots of the back, sides, and legs of the mottled leopard frogs were indistinctly outlined in broken lines, and the interspaces between the black spots were darkened by an anastomosing network of irregular flecks of black pigment. The spots, particularly on the arms and legs, tended to fuse with the mottlings between them. In each of the tanks containing mixtures of the mottled and common leopard frogs, the two

could be distinguished readily on the basis of color pattern.

In the fall and winter of 1953, shipments of both kinds of frogs collected in the prairie section of western Minnesota were received, and a series of crossing experiments was initiated in the Tulane University laboratories. The results of these experiments are described here.

Inheritance of the Color Pattern

Six series of artificial cross-fertilizations were conducted, each comprising all the possible combinations of crosses between *Rana kandiyohi* and *Rana pipiens*. Each series, designated as *A, B, C,* etc. (Table 1), consisted of the following crosses: *kandiyohi* ♀ × *kandiyohi* ♂ (abbreviated as K×K), *kandiyohi* ♀ × *pipiens* ♂ (K×P), *pipiens* ♀ × *kandiyohi* ♂ (P×K), and *pipiens* ♀ × *pipiens* ♂ (P×P). In each of the six series the procedure was as follows: a *kandiyohi* female and a *pipiens* female were induced to ovulate by frog pituitary injection. The testes of a *kandiyohi* male were dissected out into 25 cc. of 10 percent Ringer's solution and cut into small fragments, and the resulting sperm suspension was separated into two 8-inch fingerbowls. A sperm suspension, divided into two parts, was similarly prepared from the testes of a *pipiens* male. Masses of eggs from the uterus of the *kandiyohi* female were stripped alternately into a bowl containing a *kandiyohi* sperm suspension and into a bowl containing a *pipiens* sperm suspension. Likewise, eggs from the *pipiens* female were liberated into two bowls, one containing a *kandiyohi* sperm suspension and the other, a *pipiens* sperm suspension. In this manner the reciprocal fertilizations as recorded in Table 1 were effected. The eggs in each bowl remained undisturbed in the sperm suspension for twenty minutes, after which time the eggs were washed free of the fragments of testes in 10 percent Ringer's solution, and then covered with 500 cc. of 10 percent Ringer's solution. After two hours, the large egg mass in each 8-inch fingerbowl was loosened from the bottom of the bowl by means of a thin section-lifter and cut into small clusters. The eggs from each large fingerbowl were transferred to several 4-inch fingerbowls, each bowl containing

TABLE 1
RESULTS OF CROSSES BETWEEN RANA PIPIENS AND RANA KANDIYOHI

EXPERIMENT	K♀ x K♂ ↓		K♀ x P♂ ↓		P♀ x K♂ ↓		P♀ x P♂ ↓	
	K	P	K	P	K	P	K	P
A	35	9	21	17	20	26	0	35
B	7	2	9	5	6	2	0	13
C	31	14	24	19	32	24	0	24
D	56	12	21	35	28	18	0	42
E	31	5	16	25	14	18	0	40
F	37	15	26	22	18	12	0	37
TOTAL	197	57	117	123	118	100	0	191
EXPECTED	190.5	63.5	120	120	109	109	0	191
DEVIATION	6.5	6.5	3	3	9	9	0	0
CHI SQUARE	0.89		0.15		1.48			
PROBABILITY	0.35		0.70		0.22			

approximately 100 eggs in 200 cc. of 10 percent Ringer's solution. Development of the embryos was checked at regular intervals from first cleavage through metamorphosis.

A detailed account of the observations and care of the embryos in one experiment (Experiment A) is representative of all the experiments, unless otherwise specified. Experiment A was begun October 3, 1953 (Experiment B was initiated October 18; Experiment C, November 5; Experiment D, November 23; Experiment E, December 8). The development of the four groups of embryos (K×K, K×P, P×K, and P×P) at 20°C. was observed during the pre-feeding stages, stage 3 (first cleavage) to stage 25 (operculum complete). The stages of development are defined and illustrated in Shumway (1940). No differences in rate of development, as measured by the time taken for 50 percent or more of the embryos within a group to reach a given stage, could be detected among the four groups of embryos. Moreover, no abnormal development was observed in any of the groups during the pre-feeding stages. At stage 25, the onset of feeding activity, the embryos were placed in larger receptacles containing pond water and maintained at room temperature until metamorphosis took place. The tadpoles were reared in a variety of containers (enamel pans, aquaria, fish bowls, and fingerbowls). Best results, in terms of the greatest number of tadpoles successfully reared beyond metamorphosis, were obtained by utilizing enamel pans measuring 12″×8″×2″ and containing 10 tadpoles in pond water not more than an inch in depth. However, in most cases, the tadpoles were more crowded. A variety of diets was utilized, of which a regular course of slightly boiled spinach appeared to be the most satisfactory. An effort was made to change the pond water three times a week. Transformation of tadpoles began late in December and tadpoles were metamorphosing for several months thereafter. There was great variation in size in the metamorphosed young, which could be attributed mainly to the effects of crowded culture conditions.

The rearing of offspring from all sets of crosses proved to be a prodigious undertaking. In experiment A, 163 tadpoles transformed (a total of 909 transformed in all the experiments). The mortality in Experiment A, as well as in the other experiments, was estimated at 45 percent of the original number of tadpoles. That difficulty in rearing tadpoles through metamorphosis was not due to the "hybrid" nature of the tadpoles (K×P and P×K offspring) may be inferred from the fact that "non-hybrid" tadpoles (K×K and P×P offspring) seemed no less difficult to rear. In Experiment A, the number that had transformed represented 48 percent of the original amount in the K×K cross, 54 percent in the K×P cross, 62 percent in the P×K cross, and 59 percent in the P×P cross.

The results of all the experiments are summarized in Table 1. The adult color pattern first appeared at the time of metamorphosis. The transformed tadpoles from the K×K, K×P, and P×K crosses showed a sharply defined segregation into the mottled *kandiyohi* color pattern and the common-spotted *pipiens* color pattern. A total of 254 transformed in the K×K crosses, of which 197 (77.5 percent) were *kandiyohi* and 57 (22.5 percent) were *pipiens*. The K×P crosses yielded 240 metamorphosed young, of which 117 (48.8 percent) exhibited the *kandiyohi* pattern and 123 (51.2 percent) showed the *pipiens* pattern. In the reciprocal crosses, P×K, 218 transformed. Of these 118 (53.7 percent) were *kandiyohi* and 100 *pipiens* (46.3 percent). Combining the results of the reciprocal crosses (K×P and P×K), a total of 240 individuals segregated into 235 *kandiyohi* (51.3 percent) and 223 *pipiens* (48.7 percent). Only *pipiens* individuals were obtained from the P×P crosses.

The results indicate that the difference in the color pattern between *kandiyohi* and *pipiens* is due to a single gene, the

"kandiyohi" gene being dominant over the *"pipiens"* allele. All *kandiyohi* individuals employed in the experiments proved to be heterozygous for the color-pattern gene. The actual segregating population recovered from the K×K crosses fits (chi-square test) the expected ratio of 3:1. Crosses between *kandiyohi* and *pipiens* (the double recessive) yield a statistically significant ratio of 1:1. Designating the dominant (*kandiyohi*) gene as "K" and the recessive gene as "k", the crosses may be diagrammed as shown in Table 2.

Larval Differences between kandiyohi *and* pipiens

An attempt was made to relate the differences in the final phenotype to their earliest detectable ontogenetic manifestation. This involved an analysis of the stages of development of the embryos of the several crosses in order to determine the first point in development where differences in pigmentation could be discerned. During the interval between the last of the pre-feeding stages (stage 25) and the earliest feeding stage (stage I; defined by Taylor and Kollros, 1946, as that stage in which the oral sucker elevation has disappeared and four rows of labial teeth develop), chromatophores appear and become numerous on the dorsal and lateral surfaces of the tadpole. In Experiment A, it became apparent that the tadpoles after stage I in the K×K, K×P, P×K crosses were not uniform in their pigmentation. Some of the individuals in each of these crosses were "heavily" pigmented, i.e., the melanophore patches and single melanophore granules were abundant throughout most of the body. Others were "weakly" pigmented; in these the melanophore patches and pigment granules were less numerous and more dispersed. In the P×P cross, all the tadpoles appeared to be weakly pigmented. In Experiment A, as indicated in Table 3, the proportion of each type of tadpole in each of the crosses was not ascertained. The reliability of the observations made in Experiment A was tested in a more exacting way in the subsequent experiments.

In Experiments B and C, tadpoles from each cross were classified at stage VII as either "heavily" or "weakly" pigmented and separated into individual culture dishes (Table 3). Stage VII is defined in Taylor and Kollros (1946) as that period in which the hind-limb buds show no interdigital indentation. It became apparent as the embryos continued to develop that errors in classification had been made, but no change was made in the original classification. The results were as follows. Of the tadpoles in the K×K, K×P, P×K crosses that were originally classified at stage VII as weakly pigmented, 71.6 percent gave rise to *pipiens* adults and 28.4 percent to *kandiyohi* adults. Of the tadpoles classified as heavily pigmented, 96.4 percent transformed into *kandiyohi* adults and 3.6 percent into *pipiens* adults. The results suggest that heavily pigmented tadpoles represent *kandiyohi* individuals, but that not all

TABLE 2
DIAGRAM OF CROSSES INVOLVING RANA PIPIENS AND RANA KANDIYOHI

P_1	KANDIYOHI Kk × KANDIYOHI Kk	KANDIYOHI Kk × PIPIENS kk	PIPIENS kk × PIPIENS kk
F_1	KK Kk Kk, kk	Kk, kk	kk
EXPECTED	75 % 25 %	50 % 50 %	100 %
ACTUAL	77.5 % 22.5 %	51.3 % 48.7 %	100%

TABLE 3

THE RELATION BETWEEN LARVAL AND ADULT PIGMENTATION

CROSS		K♀ x K♂		K♀ x P♂		P♀ x K♂		P♀ x P♂	
TADPOLE SPOTTING / RESULTING ADULTS		WEAK	HEAVY	WEAK	HEAVY	WEAK	HEAVY	WEAK	HEAVY
EXP. A	PIPIENS	NO CLASSIFICATION MADE DISTINQUISHING FEATURES OF TADPOLES NOTED							
	KANDIYOHI								
CLASSIFIED AT STAGE 7 (43 mm.)									
B	PIPIENS	2	0	5	0	2	0	13	0
	KANDIYOHI	2	5	2	7	1	5	0	0
C	PIPIENS	9	1	15	0	15	1	17	0
	KANDIYOHI	5	10	4	12	5	15	0	0
CLASSIFIED AT STAGE 10 (54 mm)									
D	PIPIENS	8	1	15	0	11	0	14	0
	KANDIYOHI	0	14	1	11	2	18	0	0
E	PIPIENS	3	0	13	1	12	1	15	0
	KANDIYOHI	1	17	0	13	0	10	0	0
F	PIPIENS	10	2	11	0	9	1	17	0
	KANDIYOHI	0	15	2	14	0	14	0	0

kandiyohi tadpoles develop their heavy pigmentation by stage VII.

In Experiments D, E, and F, classification was delayed until stage X, when the margin of the hind-limb bud is indented between all digit primordia. Here, few mistakes were made (Table 3). Most of the *kandiyohi* tadpoles had developed their heavily pigmented pattern, and were easily sorted. The results of the classification at stage X were as follows. Of the tadpoles in the K×K, K×P, P×K crosses that were originally classified as weakly pigmented, 93.9 percent transformed into *pipiens* and 6.1 percent into *kandiyohi*. Of the tadpoles classified as heavily pigmented, 95.5 percent gave rise to *kandiyohi* and 4.5 percent to *pipiens*. Thus, the adult pigmentation differences are traceable back at least to stage X. The exceptions can be explained in part by incorrect classification.

Figures 3 and 4 illustrate the appearance of the weakly pigmented tadpoles and the heavily pigmented tadpoles at stage X. General body proportions, external structures and details of the mouthparts were similar in the two types of tadpoles. The tadpoles were measured and the structure of the mouthparts was examined after narcotizing the tadpoles with "M.S.222" (Sandoz Chemical Co., N. Y. C.).

Measurements of the body length (tip of snout to tip of tail) of the two types of tadpoles were made with a vernier caliper. The body length of 108 weakly pigmented tadpoles at stage X ranged from 51.3 mm. to 57.2 mm., the mean and standard deviation being 54.4 ± 1.52. Similar measurements of 99 heavily pigmented tadpoles at stage X indicated a range of 51.8 mm. to 56.7 mm. (53.7 ± 1.09). The difference between the means is not significant.

The structure of the mouthparts forms the basis for the identification and separation of many amphibian tadpoles. The

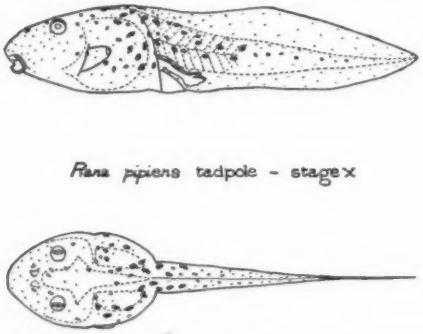

FIG. 3. A weakly pigmented *Rana pipiens* tadpole from Experiment D, showing the distribution of subepidermal melanophores that distinguishes this tadpole from the mottled leopard frog tadpole.

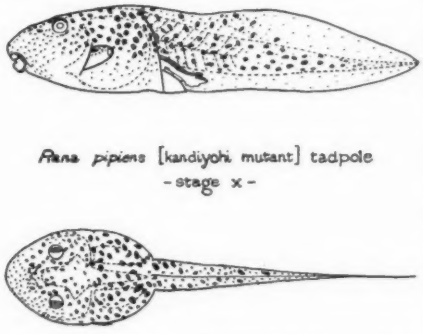

FIG. 4. A heavily pigmented *Rana pipiens* [kandiyohi dominant mutant] tadpole from Experiment D, showing the distribution of subepidermal melanophores that distinguishes this tadpole from the common leopard frog tadpole.

near-identity of *pipiens* and *kandiyohi* is reflected in the exact similarity of the mouthparts of their tadpoles (Fig. 5). The tooth-row formula in the weakly pigmented tadpoles and the heavily pigmented tadpoles was typically 2/3. Occasional variation was encountered in both types of tadpoles. In 6.5 percent of the weakly pigmented tadpoles and 5.0 percent of the heavily pigmented tadpoles, there was an additional short row on the upper labium, increasing the formula to 3/3. In 1.8 percent of the weakly pigmented tadpoles and 3 percent of the heavily pigmented tadpoles, a second upper tooth row was lacking, resulting in a 1/3 formula.

Other characters of the mouthparts were found to be identical in the two types of tadpoles. The first upper tooth row was continuous across the upper labium. The second upper tooth row was divided medially, the median space being greater in length than either lateral half of tooth row. The first lower tooth row was characteristically divided in the midline, the second lower tooth row was approximately equal in length to the first, and the third lower tooth row was invariably more than half as long as the first lower tooth row. A divided second lower tooth row was found in a few cases (2.8 percent in the weakly pigmented tadpoles and 4.0 percent in the heavily pigmented tadpoles). A row of marginal papillae was present along the sides of the upper and lower labia, and continued uninterrupted along the bottom of the lower labium. A well-defined row of submarginal papillae was present between the ends of the third lower tooth row and the point where the labia infold laterally.

Thus, the only difference detected between a *pipiens* and a *kandiyohi* tadpole was a pigmentation difference.

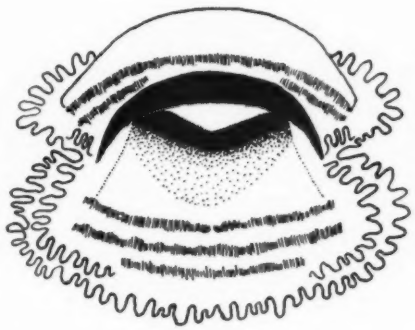

FIG. 5. Mouthparts characteristic of both *Rana pipiens* and *Rana pipiens* [kandiyohi dominant mutant] tadpoles at stage X.

Discussion

The breeding experiments have indicated that the *kandiyohi* pigment pattern results from an expression of a single dominant gene which influences pigmentation. In these experiments twelve *kandiyohi* adults were employed and all were found to be heterozygous (Kk) for the pigment-pattern gene. This raises the question of the occurrence of homozygous *kandiyohi* individuals. Pertinent to this question are the relative frequencies of *kandiyohi* and *pipiens* in natural populations. In localities in Minnesota where the two forms have been collected together, Mr. Steinhilber estimates a ratio of one *kandiyohi* to ninety-nine *pipiens*. Breckenridge (1944) has reported that collections from Minnesota of both forms contain approximately two percent *kandiyohi*. Based on these figures, the Hardy-Weinberg formula may be used to estimate the relative frequencies of homozygous and heterozygous *kandiyohi* individuals, assuming, of course, a panmictic population of infinite size. Thus, in a population consisting of one percent *kandiyohi*, one homozygous *kandiyohi* to approximately every four hundred heterozygous *kandiyohi* would be expected. If the *kandiyohi* are more abundant, forming two percent of the population, then approximately one homozygous *kandiyohi* would occur for every two hundred heterozygous *kandiyohi* individuals. If the conditions necessary for the fulfillment of the Hardy-Weinberg formula are applicable in nature, then it is not surprising that all twelve *kandiyohi* individuals tested were heterozygous. However, data are lacking as to the history of the populations, the extent of differential migration, selection, and mutation rates.

An attempt was made to distinguish phenotypically between homozygous (KK) and heterozygous (Kk) transformed offspring. Theoretically, two-thirds of the *kandiyohi* young from K×K crosses should be heterozygous, and one-third homozygous. However, no consistent combination of phenotypic characters separating the two genotypes could be found. There was extensive individual variation in intensity of color in the metamorphosed young, but the variation did not readily fall into two clearly discernible classes. Variation was also encountered in the size and arrangement of the pigment mottlings, but again the problem arose as to how the various kinds of minute individual differences in pigmentation could be best combined into a single conclusive judgment differentiating a KK from a Kk. An objectively obtained basis for judgment can only be derived from backcrossing experiments, but this is dependent, regrettably, upon the ease with which sexually mature frogs can be reared in the laboratory.

Only a few investigators have attempted to analyze the inheritance of traits in amphibians, and this is understandable in terms of the relatively slow generation time and the difficulties encountered in rearing amphibian young to sexual maturity. Rostand (1951) has recently summarized the literature on genetic analyses in amphibians. The case of recessive albinism in amphibians, found by several workers, is well known. Among other cases, Moore (1942) has demonstrated that the non-spotted leopard frog, *Rana pipiens* [burnsi mutant], differs from the common leopard frog, *Rana pipiens*, by a single dominant gene that affects pigmentation. In addition, Moore (1943) has shown that the mutant gene for "non-spotting" is dominant to its allele for "spotting" in three distinct species, *Rana pipiens*, *R. palustris*, and *R. areolata*. Goin (1947) has demonstrated by breeding tests that the two distinct color patterns of Ricord's frog, *Eleutherodactylus ricordi planirostris*, striped and mottled, are due to the allelic genes S (striped) and s (mottled), with S dominant to s. In a later study, Goin (1950) has presented evidence that three pattern variations in *Eleutherodactylus nubicola*, dorsolateral stripes, picket, and mid-dorsal stripe are simple Mendelian

traits with the gene for each situated in a separate locus. Each of the above cases, as well as the present study, has been demonstrated to be based on simple Mendelian inheritance; but undoubtedly, as more genetical work is undertaken, complicating factors, such as modifying genes, will be uncovered.

The results of the present investigation are of particular interest to systematists. It is clear that *Rana kandiyohi* does not represent a metachrotic condition or phase of *Rana pipiens,* nor should it have the status of a species or subspecies. *Rana kandiyohi* is simply a dominant mutant form of *Rana pipiens,* and should be referred to as *Rana pipiens* [kandiyohi dominant mutant].

Summary

The results of breeding tests have indicated that the mottled leopard frog, *Rana kandiyohi,* differs from the common leopard frog, *Rana pipiens,* by a single dominant gene that influences color pattern. The adult color-pattern differences are heralded in the larval stages; the two types of tadpoles are distinguishable by stage X (hind-limb buds show interdigital indentations), and possibly earlier. *Rana kandiyohi* should be retained in synonomy with *Rana pipiens* and be designated as the [kandiyohi dominant mutant].

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Biological Races of Caspian Sturgeons

The co-existence of as many as four populations of one species of sturgeon that differ from each other primarily in reproductive behavior is a phenomenon which merits thoughtful consideration. The most recent summary of the investigations of the reproductive biology of these anadromous fish is an article written in Russian by N. L. GERBILSKII—*"Intraspecific biological groups of acipenserine fishes and their reproduction in the lower regions of rivers with regulated flow,"* Rybnoe Khoziaistvo, *27(4):24–27, 1951.* A. PETRUNKEVITCH *has prepared the literal translation of Gerbilskii's paper that appears below. As, however, the author considered these phenomena primarily from the standpoint of a pisciculturalist, the translation is preceded by a foreword—by* GRACE E. PICKFORD—*which presents the background for these investigations as well as their general implications.*

Foreword

TWENTY years have elapsed since Berg (1934) published his well-known article on vernal and winter races of anadromous fishes. In his conclusion he stated that the vernal and winter races of the most diverse groups of anadromous fishes show a series of features in common: (1) Winter fish spend the coldest time of the year either in the river itself, or in the sea close to the river mouth. Vernal fish are said to enter the river at higher temperatures. (2) During the coldest season of the year the winter races pass through a stage of vegetative quiescence, eating little or nothing. Many hibernate in holes. Vernal races have, at the most, only a short period of vegetative quiescence, and do not hibernate. (3) The vernal races spawn in the same season in which they enter the rivers. The winter races spawn the following year, after a long interval of time. (4) The winter race usually spawns earlier than the vernal race, i.e. in a given year they mature earlier. (5) The winter race goes higher upstream than the vernal race. (6) The winter race is usually larger than the vernal race. (7) The winter race is usually more fertile than the vernal.

It is not our purpose to review this article, which is available to the interested reader in German translation (Berg, 1935), but to call attention to more recent Russian research on the biological races of acipenserine fishes. This recent literature came to our attention during the course of an attempt to review the Russian contributions to the subject of fish endocrinology, and all of it is concerned with the application of the method of hypophysis injection in the artificial induction of spawning. The method is not successful unless the fish have reached a certain stage of sexual maturity and, as will be seen from Gerbilskii's article, not all the biological races of a given species enter the river in a suitable stage for injection. The Russian workers have been primarily interested in conservation measures, undertaken in connection with the construction of hydroelectric plants which interfere with the normal upstream spawning migration of the fishes. This point of view is the one that is emphasized in the review article by Gerbilskii (1951), a complete translation of which follows. The translation of this, and other Russian articles on the same subject, was dictated to me by Professor A. Petrunkevitch of the Osborn Zoological Laboratory, Yale University, who is responsible for the final draft of the manuscript. Gerbilskii's article is not accompanied by references, except to Lysenko, but a number of these have been added to enhance the value of the translation.

It was shown by Gerbilskii (1950, and

earlier references therein) and his collaborators that the biological races of the Kura [1] osetr (*Acipenser güldenstädti persicus* Borodin) are more complicated than was realized in the earlier work of Berg. An early vernal race enters the river in spring with gonads in an advanced state of maturity. Such fish can be induced to spawn with a single injection of hypophysis extract. Following this a late vernal race enters the rivers with the gonads not yet fully mature; such fish do not respond to hypophysis injections. They migrate 600 km. upstream to the Mingechaur spawning grounds and do not become sexually mature until midsummer. During the summer, osetr of the winter race enter the river; these fish, which are far from sexual maturity, will hibernate in holes in the river and do not spawn until the following year. Finally, in autumn, there again appear fish with mature gonads, ready to spawn.

This work was quickly followed by similar studies of other species. Petropavlovskaia, 1950) was able to induce spawning in the vernal race of the Kura beluga (*Huso huso* (*Linn.*)). Titarenko (1950) studied the Volga sevriuga (*Acipenser stellatus* Pallas) and was able to show that fish of the vernal race could be used for piscicultural purposes by artificial induction of spawning. In a later paper by Titarenko and Ulezko (1951) this work was extended to include the early vernal race of the Volga osetr. Gerbilskii, Barannikova, and Kazanskii (1951) turned their attention to the problem of obtaining eggs for autumn rearing. Eggs may be obtained from sexually mature Kura osetr of the late vernal race in summer, at the Mingechaur spawning grounds which are far upstream. The larvae must then be transported by air to the down-river stations for rearing. Alternatively fish of the late vernal race, taken when they enter the river in spring, may be kept in ponds or canals at the down-river plants until late August when they are ready to spawn. There are technical difficulties in keeping the fish, but this is a separate problem, and eggs that are fertilized in hot weather, at temperatures of over 22°–24° C., develop abnormally. On the other hand, fish of the autumn group enter the river with mature gonads, and such fish can readily be induced to spawn by the method of hypophysis injection. This aspect was further investigated by Kazanskii (1953) who studied the Kura osetr and showed that when fish of the autumn race are kept in captivity they will spawn naturally as the temperature falls to 16°–17° C. in September. This contribution is of particular interest since it establishes definitely that "vernal fish of the autumn migration" spawn in the same season, as was already suspected from the condition of the gonads, and do not pass the winter in a state of hibernation to spawn in the spring. On the other hand, Barannikova (1954) reports that Volga osetr of the autumnal run, which enter the delta in late autumn with the gonads in an advanced state of maturation, nevertheless do not spawn at that time but are a winter race that hibernate in holes in the river. Such fish were kept in artificial ponds in the delta of the Volga and were induced to spawn in the following spring, after hypophysis injection. Barannikova considers it possible that this race might hybridize with fish of the early vernal race which enter the river in spring and spawn at about the same time in the same regions.

We have thus a complicated situation that differs in every river system. For any given species there may be as many as four different biological races, entering the river at different times of year, and as a rule spawning at different times and in different regions. As pointed out by the Russian investigators, this is an adaptation that ensures full utilization of the spawning grounds. Thus the early vernal and autumnal races of the Kura osetr spawn in the lower regions, but at

[1] The river Kura arises in the mountains between Georgia and Azerbaijan and flows eastward into the Caspian.

different times of year. On the other hand, the winter and late vernal races go further upstream but the former spawns earlier than the latter. We appear to be confronted with a case of sympatric raciation in which the isolating factor is, on the one hand, a partial geographical separation of the spawning grounds, and, on the other hand, a seasonal difference in the time of spawning. Berg has pointed out that the winter races are usually of larger size and produce more eggs, but, in general, morphological differences other than those associated with the state of sexual maturity are slight.

Each river system has its own proportions of the different biological races; in the Volga, for example, the chief run of sevriuga is the vernal race while the chief run of osetr is a winter race. Such observations suggest that there may be a balance resulting from interspecific competition within a given river basin.

There is another aspect of the problem that is of general biological interest. The early vernal sturgeons spawn on a rising temperature, as does the winter race; under the same conditions of rising temperature, the late vernal sturgeons mature slowly and do not spawn until midsummer; the autumn group enters the river in warm weather and does not spawn until the temperature falls to 16°–17° C. Clearly it is not possible to generalize as to the nature of the stimulus that brings about maturation of the gonads and subsequent spawning. Each race is attuned to its own special sequence of environmental changes, and the only common factor is the familiar rule that a biological stimulus is an environmental change.

In regard to the origin of the biological races, we cannot agree with the Russian workers who, following the teachings of Lysenko, attribute the formation of seasonal races to the direct influence of the environment. There is too little experimental evidence regarding the stability of the seasonal races but, after reviewing the problem, Berg came to the conclusion that they represent distinct breeding populations. A vernal fish cannot, for example, change into a winter form, and the offspring belong to the same biological race as the parents. This was experimentally demonstrated by Rich and Holmes (1929) who transported eggs of spring and fall chinook salmon and marked the fry before release. Adults of spring fry released into a river in which only autumn salmon occur were recaptured in spring and, conversely, autumn forms were recaptured in late summer. A majority of the latter group returned to the stream in which they had been reared, and neither group returned to the place of spawning. Thus there is a strong tendency for the fish to return to the stream in which the fry were released, but the seasonal character is not changed. Recent work of Hasler (1954) has shown that minnows can recognize the water of the parent stream by its odor, and it is therefore possible that migratory fish are imprinted with the characteristics of the environment in which they were reared. Since the Russians are now engaged in an extensive artificial rearing of fry of various species it will be interesting to learn whether new biological races, imprinted with the hatchery environment, will appear.

In the translation which follows, the Russian names of the species have been retained: the osetr is the Russian sturgeon, *Acipenser güldenstädti* Brandt; the sevriuga is the stellated sturgeon, *Acipenser stellatus* Pallas; the beluga is the giant sturgeon, *Huso huso* (Linn.).

Intraspecific Biological Groups of Acipenserines and Their Reproduction in the Lower Regions of Rivers With Regulated Flow

THE piscicultural and biological study of osetr, sevriuga, and beluga of the southern rivers of the Soviet Union (Kura, Volga, and Don) has shown that the so-called "schools" of these fish (for example, the "school" of the Kura osetr, or the "school" of the Don beluga) are not of uniform composition. Biologically different intraspecific groups of these fishes are found not only in different seas and rivers but also—what is especially important—within the limits of a single basin.

The peculiarities of these biological groups are extremely important for pisciculture, while the knowledge of intraspecific biological groups of acipenserines in each basin forms the foundation of acipenserine conservation measures in connection with hydroconstruction. The development of the concept of intraspecific biological groups progresses in close association with the requirements of pisciculture; therefore the creative participation of workers of piscicultural plants and of the production laboratories of Glavrybvod is especially important in its elaboration.

The time is ripe to formulate the basic principles of this doctrine, to determine the methods common to all rivers for elucidating and characterizing pisciculturally the intraspecific biological groups, and to show by examples the advantages which pisciculture can derive from a knowledge of intraspecific biological groups.

We define as a biological group the complex of individuals belonging to a single species but differing from other biological groups of the same species by peculiarities of the biology of their development.

In the world of fishes these differences are referable primarily to phenomena connected with the process of reproduction (differences in the sexual cycle, in the time and locality of spawning, in spawning temperatures, in the condition of the producers [spawners] during their migration from the sea into the rivers, etc.). Changes in the condition of development of the sexual cells and in the seasonal cycle of the reproductive system form the basis of the differences in the process of reproduction in representatives of different biological groups.

The differences between the biological groups within the limits of a species are not restricted to peculiarities of sexually mature individuals. The differences in the process of reproduction, for example in regard to the condition of maturation of oocytes and spermatozoa, of the embryonic development and formation of the fry, cannot help inducing as a consequence some peculiarities in the biological development of the progeny of different biological groups. Thus there arise in nature biologically diverse, and hereditarily more or less stable groups within a species.

The intraspecific biological groups within the limits of a basin are of particular interest for pisciculture. The presence of such groups permits species to make more effective use of the spawning grounds and of the food resources of the basin, which are subject to seasonal changes both of a qualitative and of a quantitative nature. *Consequently the presence of biological groups must favor the numerical increase and general welfare of a species in a given basin.*

Such biological diversity within the limits of a species is not an attribute of fish alone, but is a phenomenon of a general biological order. Academician T. D. Lysenko writes: "The profusion of varieties is assured by a many-sided zoological

adaptation of the species concerned, promoting its flourishing and preservation. The more numerous the varieties of the one or the other species, and the richer the intraspecific diversity of the population, the greater the possibilities that the species with all its varieties will flourish." [2]

The elucidation and the piscicultural characterization of intraspecific biological groups of fishes within the limits of a basin have a decisive importance for the elaboration of methods of plant production. The elaboration and perfection of the technology of rearing fish (for example, the establishment of a rational plan of work in piscicultural plants, and the solution of the problem of the feasibility of repeated use of basic facilities during the course of a single piscicultural season) can be achieved only on the basis of a profound knowledge of the peculiarities of reproduction of each object of pisciculture.

Having defined the meaning of an intraspecific biological group we must, to avoid confusion, accept a general terminology for the notation of such biological groups.

Following the example of L. S. Berg, we shall call those biological groups that hibernate in the river before spawning, winter groups—"the winter biological group." The transitory fish which spawn after entering the rivers, before the advent of winter (i.e. in spring, summer, and autumn), we shall call vernal—"the vernal biological group." However, investigations have shown that these definitions do not comprise the entire diversity of intraspecific biological groups of acipenserines within the limits of a basin. For this reason it becomes necessary to add to the two above-mentioned basic definitions distinctive biological characteristics, for example, "early" or "late" vernal osetr, or "vernal of the autumnal migration." The meaning of these terms will be clear from examples given below. Of course, with the growth of knowledge this terminology will be improved and elaborated.

The work of elucidation and piscicultural characterization of biological groups of acipenerines is accomplished according to the following scheme.

1. The character of the migration of the producers of a given species is studied in the lower regions of the river. In this respect, an analysis of the numerical indices of capture in the largest down-river fisheries, arranged by months and decades for an entire year, is of great help. Such an analysis determines the presence of one, two, or more peaks of migration. The existence of periods of migration, well delimited in time, bespeaks the presence of biological groups of the given species in the basin which is under investigation.

2. The condition of the producers at the time of their entrance into the river from the sea is subjected to an analysis for the duration of an entire year. Special attention is given to the degree of proximity to the spawning condition. In this respect the most important indices for acipenserines are the weight and size of the eggs, the degree of development or absence of noticeable adipose tissue in the ovaries and testes, the degree of development of adipose tissue in the muscles of the back and belly; attention is also paid to the ratio between the weight of the ovaries and the total weight of the body. These data, determined at autopsy of the fish on floats, are supplemented by the results of a histological analysis of the ovaries and testes, made for the determination of fine distinctions in the process of development of the oocytes or spermatocytes in representatives of different biological groups.

3. An especially important criterion for the allocation of a given specimen to this or to that biological group is the positive or negative reaction to hypophysis injection. Taken altogether, the above-mentioned features permit a characterization

[2] *Pravda*, Nov. 3, 1950. An article entitled "Advances in the science of biological species."

of the basic biological groups of a given species in a given river.

4. The extension of the spawning zones of the studied fish in a given river is determined, and a calendar of spawning in various regions of that zone over a period of years is prepared.

In this briefly narrated procedure for the elucidation of the intraspecific biological groups the leading role is played by the determination of the degree of maturity of the migrating producers in the lower regions of the river. All the other data serve to lay more complete foundations for the conclusions made on the basis of such an analysis.

In applying such a procedure we were able, for example, to recognize four biological groups of the Kura osetr—the early vernal osetr, the late vernal osetr, the winter osetr, and the vernal osetr of the autumnal migration. The early vernal osetr enters the river Kura early in spring in a condition very close to maturity, and spawns soon after its entrance into the river. The late vernal osetr enters from the sea following the early vernal one in a condition still remote from spawning, migrates far up the river Kura, and spawns only in August. The winter osetr enters the river Kura in summer, hibernates in the river, and spawns only the next spring. The vernal osetr of the autumnal migration appears in the catches of down-river fisheries only in September, is very close to the spawning condition, and evidently spawns before the winter cooling (see Table I).[3]

Let us give another example. The Don beluga enters the river from Tagonrog Bay at different times of the year and in very different conditions. In spring (March to the beginning of May) the beluga producers captured here are very close to the spawning condition in respect to the development of their sexual products. As V. N. Petropavlovskaia and P. A. Samsonenko have shown, it is possible to get mature eggs and sperm from such beluga with the aid of hypophysis injection, and to rear the progeny directly after the capture of the producers. This beluga belongs unequivocally to the vernal biological group.

However, following this beluga, producers enter in a totally different condition. Thus, according to the data of A. A. Meleshko, the quantity of eggs in a single gram from a vernal beluga fluctuates between 36 and 50, while in the beluga following it the weight of the eggs is half as great (78 to 105 per gram). This beluga will spawn after hibernation in the river only in April and May of the next year.

In the lower fisheries of the Don, beluga with large ova are again captured after the second decade of September. The development of the sexual cells in the males of this beluga is also completed at this time. The problem is to decide whether this is a winter beluga or whether, like the vernal osetr of the autumnal migration in the Kura, it is capable of spawning in autumn.

Data concerning the intraspecific biological groups established for a single basin cannot be applied directly to fish of the same species but reproducing in a different river, because other biological groups may occur there or corresponding biological groups may have a quite different commercial importance. For example, there exists among the Volga osetr a *tuvodnaia* biological group (one which migrates only within the limits of the river) whereas in the Kura osetr such a group is lacking. The winter biological group of the Volga and Kura osetr forms a considerable portion of the total count, while the Don winter osetr is less than one-twentieth as abundant as the vernal osetr of the same river. Such considerable differences in the biological groups of the same species in different basins may be explained primarily by the conditions of

[3] It is very useful to prepare such tables in describing biological groups. As the data characterizing biological groups increase and become more refined, and as the procedure of rearing develops, the details of such tables will be further refined and supplemented.

TABLE I—BIOLOGICAL GROUPS OF THE KURA OSETR AND METHODS OF THEIR PLANT PRODUCTION

NAME OF BIOLOGICAL GROUP	TIME OF ENTRANCE INTO RIVER KURA	CONDITION OF SEXUAL GLANDS AT TIME OF ENTRANCE	TIME OF SPAWNING	SUPPOSED PLACES OF SPAWNING	SPAWNING TEMPERATURE °C	PERCENT OF SCHOOL FORMED BY GROUP	METHOD OF PLANT PRODUCTION	REMARKS
Early vernal osetr	February to first half of May. Main migration in April	Completed IVth stage. The egg of definitive size. Adipose tissue of ovary not visible. Spermatogenesis completed.	May	Lower regions of spawning zone	13–15	ca. 30–35	Producers from Maiak I and II, April. River cages without prolonged keeping, or early segregation and keeping until 13° C. Method of hypophysis injection. Pond-rearing of fry (May to June).	Osetr of this group have been established as an object of production with release of 2-month-old fry.
Late vernal osetr	May to June	Fatty osetr. Eggs of definitive or almost definitive size. Fat layers in gonads.	Second half of August and beginning of September	Upper regions of spawning zone	23–18		Producers from Maiak I and II are kept until September in special ponds or canals. Method of hypophysis injection. Pond-rearing of fry (September to October).	The producers of this group may fully assure the autumn pond-rearing of fry.
Winter osetr of the summer migration	June to July and part of August	Fatty osetr. Eggs far from the definitive size. Strong development of fatty tissue in ovaries and testes.	April and part of May	Upper regions of spawning zone	12–15	50–60	Early spring capture of producers at the lower dam MGES. Method of hypophysis injection. Release of larvae and their transportation in part to down-river plants for rearing.	Producers taken only at spawning temperatures and immediately by the lower dam MGES, so as not to interfere with possible spawning of these producers in the under water [bief] of the Kura between dams.
Vernal osetr (?)[1] of the autumnal migration	Part of August to September	Completed IVth stage. Fatty tissue in ovaries not visible.	Evidently October to November	Lowest regions of spawning zone	17–12 (?)	5–10	Producers from Maiak I and II. Method of hypophysis injection. Pond-rearing of fry (September to October).	Ripe eggs obtained in September, and fry reared in Autumn. Males and females mature in autumn after hypophysis injection.

[1] This query (?), which appears in the original article, could now be omitted since, as mentioned in the Foreword, Kazanskii (1953) has since shown that the vernal osetr of the autumn migration spawn naturally in September.

development of the species, closely connected with the history and present peculiarities of each basin. In the interests of pisciculture all these differences must be elucidated within as short a period of time as possible.

The use derived by pisciculture, especially in connection with hydroconstruction, resulting from a knowledge of the intraspecific biological groups of acipenserines within the limits of a basin is very great.

As a consequence of the recognition and piscicultural characterization of the late vernal osetr and of the vernal osetr of the autumnal migration, we have been able to settle definitely the question of supplying the Kura osetr plants with stock material for the autumn rearing of fry, thus increasing sharply the productivity of the plants, reducing considerably the expenditure of capital on their construction, and considerably lowering the expense of production.

B. N. Kazanskii has developed a procedure for rearing sevriuga of the autumnal biological group on the basis of his analysis of the biological groups of Kuban sevriuga. Experience has shown that such winter sevriuga captured in autumn, although very far from spawning condition and with oocytes remote from their definitive size, will not only withstand well a prolonged sojourn in ponds (until spring), but at the same time will pass into a completed fourth stage of maturity and produce mature sexual products in spring under the influence of hypophysis injection. Fry of such sevriuga were reared in the spring of 1950.

Owing to the recognition of the early vernal osetr, with which the pisciculturists in the Volga delta were unfamiliar, A. I. Titarenko has proved experimentally the possibility of mass production of osetr by using producers captured commercially.

As the result of an analysis of intraspecific biological groups of the Don beluga, it became clear that the vernal beluga, with the exception of an infinitesimal number of specimens, succeeds in passing to the spawning grounds before the closing of the Kochetov locks and that the arrest of the beluga of the winter biological group does not cause any irregularities either in the development of their sexual cells or in the seasonal cycle of the sex glands (V. N. Petropavlovskaia). These data are very necessary for the elaboration of measures of plant production of beluga in connection with the great Don hydrostructures.

A number of such examples have already been accumulated illustrating the utility of the doctrine of intraspecific biological groups for the production of fish reserve stock in connection with hydroconstruction.

The problem of the science of fish husbandry, and especially of pisciculturists and workers in our production laboratories, is to give a detailed analysis of intraspecific biological groups of all migratory fishes in the basins of those rivers the flow of which is subject to regulation.

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A number of articles in out-of-the-way Russian fishery publications, such as *Trudy Laboratorii Osnov Rybovodstva,* are not available in the United States, but it is believed that the references cited above (all of which have been consulted) cover the more essential contributions. The work of Meleshko, quoted by Gerbilskii, has not been traced, and the work of Petropavlovskaia and Samsonenko is apparently covered in the article by Petropavlovskaia (1950) who states that P. A. Samsonenko collaborated in the investigation. The quotation from Lysenko corresponds closely with its counterpart in the English version of the article listed above. The exact wording of the English version of these two sentences is as follows: "The profusion of varieties is the result of the many-sided ecological adaptivity of the species concerned; it promotes the well-being of the species and tends to preserve it. The more varieties within a species and the more diversified its intraspecific populations, the more certain the species and all its varieties are to thrive, through the agency of, for instance, cross pollination." Gerbilskii has apparently substituted "zoological" for "ecological," and has omitted the reference to cross pollination.

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ADDENDUM

In an article received since the above manuscript was submitted for publication, Derzhavin (1953) summarises his objections to the theory of biological races and to the method of hypophysis injection. In a succeeding article in the same publication, Gerbilskii (1953) again reviews the problems and replies to the criticisms of Derzhavin. According to Derzhavin there is only one breeding race of a given species in a given river system, and the different times of entry into the river are determined by a variety of external circumstances. It is supposed that the ancestral form was a river species, like the "tuvodnaia" race of the Volga osetr, and that migration into the sea was an adaptation associated with an extension of the feeding area. The sea pastures are situated at different distances from the river mouth and this leads to variations in the time of entry into the river. Furthermore, some species, like the sevriuga, beluga, and ship, are intolerant of high temperature, and in the Kura, at the southern limits of the range, do not enter the river in summer. Thus there are two migration peaks, in spring and autumn. Contrary to the claims of Gerbilskii, it is maintained that the Kura osetr, which withstands warm temperatures, retains the single migration peak in midsummer. Derzhavin supposes that the run, the acipenserine biological

year, begins in autumn. The numbers of fish which enter in autumn can be shown to depend on the volume of water in the river; in dry years the run is smaller, in wet years greater. The number of autumnal fish that succeed in spawning before the temperature falls to 10° C. in October–November also depends on external conditions, and those which do not spawn in autumn must hibernate in the river. Thus there is no real distinction between the "winter race" and the "vernal race of the autumnal migration." Derzhavin maintains that there is a progressive increase in average egg-size from autumn onwards, but Gerbilskii points out that this is based on the monthly means for all fish and that a more careful analysis shows clearly that, for example in the Kura osetr in spring, two completely different groups can be recognised. The taking of mean values merely beclouds the issue.

Among the numerous objections which Derzhavin raises in criticism of the theory of hereditary biological races, there are some other points of interest. Most reasonably, he points out that the comparison with vernal and winter races of plants is inappropriate since vernalisation affects the development of an embryo that has already begun to grow. Also, as noted in a footnote to the translation, Gerbilskii omits the most important statement at the end of his quotation from Lysenko, *viz.* that the possibility of the flourishing of a (plant) species is secured in the first place by cross pollination. If applied to an animal this would mean the crossing of as many varieties as possible. Thus the establishment of hereditarily stable biological groups with segregated spawning regions would have the opposite effect and impoverish the potentials of the species. Neither author mentions current Western concepts of the roles of population size and partial isolation on the establishment of races, subspecies, and species.

Another interesting, and apparently valid, criticism of Gerbilskii's scheme concerns the location of the spawning areas in the lower or upper regions of the spawning zone. According to Derzhavin, there are two spawning regions in the Kura river basin; the Mingechuar region extends for more than 100 km. along the river Kura, the Karadonly region not more than 30–40 km. along the river Araks. The major spawning grounds are even more restricted to gravelly regions in the vicinity of the villages of Mingechaur and Karadonly respectively. The designation of upper or lower spawning regions appears to have little meaning and was probably added by Gerbilskii as an afterthought, based partly on theoretical considerations and partly on the erroneous assumption of the existence of spawning grounds in the lower part of the Kura. Derzhavin also points out that within the not too distant past (2000–3000 years ago) the river systems of the Kura and Araks were separate and that racial differences might persist in the present mixed population.

Photographic Light

(Concluded from page 74)

prong of which has no other function than to prevent its insertion into an ordinary electric outlet.

The apparatus has also been useful for photographing a variety of other subjects than those for which it was originally designed. It has been used for copying, where it gives a most satisfactory soft lighting which produces a very good photocopy. With the aid of extension tubes or supplementary lenses it gives fine illumination for the photography of small objects of all kinds, where the lighting desired is such as to bring out all the finest details of form and texture, rather than strong or dramatic side illumination. The only limitation on its successful use is that, because of its relatively low power, it cannot be used for subjects which require short exposures, such as living animals or objects in motion.

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Points of View

On Subspecies

During the past twenty years much has been done to clarify the species concept and to establish criteria for its recognition. Discussions of speciation repeatedly underline the importance of infraspecific categories, but no generally acceptable set of criteria for the subspecies, either as a biologic concept or as a taxon, has yet been devised. The purely nomenclatural guidance found in the International Rules quite rightly fails to define the subspecies or to suggest a basis for taxonomic or biologic decision. In view of the process we call speciation and in view of the enormous diversity of infraspecific variation, it is not surprising that the subspecies as a taxon has been used in a heterogeneous fashion by systematists collectively. At one time or another, by one student or another, the term subspecies has been applied to physiological variations, genetic minorities, micropopulations, seasonal generations, geographic populations, aberrations, and almost any other kind of grouping regarded as being infraspecific.

It may not be amiss to state the obvious fact that the systematist must decide three successive independent but related questions: (1) the organisms under consideration must be analyzed biologically, (2) the organisms must be assigned to a taxonomic level, (3) the taxa must be named or not named in accordance with the International Rules.

The first of these three questions is the most difficult; the last is the easiest. A satisfactory decision on the biologic status of a group of organisms can be reached only with sufficient specimens and sufficient information about them. As Hubbell (1954, *Syst. Zool.*, Vol. 3, p. 113) points out, entomological taxonomists, among others, often must work from small numbers of specimens and without desirable life-history and genetic information. As a consequence, step number 1 may be of necessity completed inadequately, and the study may begin in fact with step number 2. On the other hand, the very human weakness sometimes called the "mihi-itch" may lead to an improper decision at step number 2, even though step number 1 may have been dealt with soundly.

In any event, the use of the subspecies as a taxon has been most inconsistent. It is a healthy sign that systematists now are being articulately unhappy with the situation. It is even healthier that remedies are being suggested. But before undertaking prognosis and cure, better diagnosis is needed.

Among others, Wilson and Brown (1953, *Syst. Zool.*, Vol. 2, pp. 97–110) argue that there is no such thing as a biologic subspecies, that therefore both the taxon and the rules relating to it are "inefficient and superfluous." They seize the opportunity to recommend eliminating "cumbersome appurtenances—the types, the tinted labels," and one suspects that impatience with taxonomic and nomenclatural procedure in general influences biologic judgment.

Edwards (1954, *Syst. Zool.*, Vol. 3, pp. 1–20), no less perturbed by the appalling misuse of the subspecies category, believes that the difficulty lies with the taxonomist rather than with the taxon. He seeks to define a subspecies concept in harmony with the current species concept: "subspecies are natural, obviously different populations, the members of which would cross-breed rather freely *if* they occurred sympatrically and synchronically under natural conditions. . . . But subspecies must *always* be allopatric and allochronic." Perhaps the most prom-

inent weakness in this definition is its failure to specify degree of difference other than that it must be obvious. However, Edwards' discussion views with disfavor those subspecies which are based on statistical conformation, and excludes from eligibility as subspecies all phenocopies, Mendelian variants, polymorphic variants, aberrations, sports, freaks, and other abnormal individuals. Were Edwards' definition and exclusions to be used, certainly a great deal of the present confusion would resolve itself. It would appear that Edwards has taken a useful and reasonable step in the right direction.

Brown and Wilson (1954, *Syst. Zool.*, Vol. 3, pp. 174–176) aver that "Edwards ignores the central argument against the objective subspecies: (1) the apparent universality of non-concordance in geographic variation, and (2) the extreme difficulty and arbitrariness inherent in the delimitation of populations in terms of real or presumed geographic discontinuities." Argument (1) is not supported by my own experience. I see no universality of non-concordance in geographic variation. This is not to say that I believe that all species of all organisms can be divided neatly into subspecies, each recognizably different from all others and at the same time geographically arranged. I merely state that in the animals I have studied this is the usual condition. Argument (2) really is an opinion rather than an argument. I cannot understand why there is any graver difficulty or arbitrariness in delimiting populations in terms of geographic discontinuities in order to evaluate subspecific status than there is, for practical purposes, in evaluating specific status in terms of the genetic organization and potentiality for hybridizing. If these things were easy, taxonomy could be delegated to clerks and stenographers, and all of us could turn our trained scientific minds to areas of greater challenge.

In this whole connection, the lepidopterous family Ithomiidae is instructive. My work with these butterflies has been, of necessity, with museum material. Thanks to the cooperative spirit of museum officials it has been possible for me to study all the specimens from all the major and some of the minor collections, brought together in one place. About 20,000 specimens have afforded data for analyzing 45 genera and 349 species.

Generic diagnosis in the Ithomiidae is based on variation in structure of wings, legs, antennae, and male genitalia; specific diagnosis is based on these plus differences in pattern *anatomy*. Morphologic criteria for species have been used exclusively, since the theoretically final test—will two presumptive species interbreed freely if made artificially sympatric and synchronic?—never has been available to me. From these morphologic data I have had (in Edwards' words) to "theorize correctly as to the degree of reproductive isolation" as best I might. Admittedly, this procedure lacks the definitiveness of experimental cross-breeding, but its quite usual application in lieu of the possibility of applying the genetic test makes it somewhat less than the "extreme contention" as viewed by Brown and Wilson (1954, *loc. cit.*).

Disregarding color and pattern of the wings, all Ithomines having identical structures in all other respects I have called a species. No case of sympatry has arisen within these species, although in many instances the species may range from southern Mexico to northern Argentina and be strongly polytypic in pattern and coloring. My problem is simplified by the lack of clines in the variation of coloring and pattern, as a rule. Color and pattern in the Ithomines seem to be much more strongly influenced by the phenomenon called "mimicry," with convergent and parallel evolution contributing further complication. It is not facetious but all too frequently true of these butterflies that if two series are closely similar they probably are unrelated, but that if they are quite different in appearance they may be the same species!

What is to be done with these geographically correlated variations in color

and pattern? Each cannot be elevated to the status of species. The morphologic evidence indicates conspecificity among long geographic series of forms. There is no practical way to obtain evidence on reproductive isolation. I have called them subspecies.

Some Ithomine genera are strong fliers; there is interbreeding along their subspecific boundaries. Other Ithomine genera are unadventuresome inhabitants of the underbrush; there is no evidence of interbreeding between subspecies. The difference between these two situations evidently lies in the flight habits and area of individual range of the insects concerned, rather than with any difference in evolutional attainment. In some cases the subspecific distribution is discontinuous, suggesting the well-known "drying up" situation, and again there is no intersubspecific gene exchange. There is no reason for assigning subspecific status to one of these kinds of situations and not to the others.

Wilson and Brown (1953, *loc. cit.*) believe that taxonomists must now choose between two possibilities: (1) to retain the subspecies as a taxon to which may be assigned any and all infraspecific variants and populations, or (2) to eliminate the subspecies entirely as a recognized taxon. I most emphatically agree with them and with many other taxonomists that the first of these choices is undesirable. But if the second choice is selected, as they recommend, all these morphologically identical but differently patterned and colored Ithomine populations will have to be elevated to species rank. This will make present species into species groups, present species groups will have to be genera, and the genera will become tribes—all of which would be absurd. Most of the latinized names now used for subspecies go back fifty years or a century or more and first were used to designate species. All would have to be accounted for in the synonymy, even were the subspecies to be eliminated or even were vernacular designations or descriptions to be used for the subspecies. Absolutely nothing would be saved in the bibliography department.

The effect of eliminating the subspecies in the Ithomiidae would be a downward revision of taxonomic concept and would merely introduce chaos at all levels. Confusion would be injected into the classification of a family where earlier confusion has been eliminated only by the use of the subspecies.

I do not find the system of trinomial nomenclature inefficient and superfluous for reference purposes. I have found it exceedingly useful in the analysis of geographic variation as well as in the analysis of evolutional level. The fact that the subspecies as a taxon has been used for manifestly inacceptable populations or fractions of populations does not invalidate the subspecies as a biologic concept. Nor would any useful purpose be served by eliminating the subspecies because it is not a useful taxon in certain groups of organisms or because clinal variation is not expressed well by using the subspecies.

Since it is evident that the subspecies is a valuable taxon in classifying certain organisms, and since there is still the probability that the subspecies has biologic validity and meaning, at least in some organisms, it would appear that a continued effort must be made to define the subspecies, refine the criteria, and discourage misuse of the taxon.

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Zoogeography

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CURT KOSSWIG, now Professor of Zoology at the Zoological Institute, Hamburg, Germany, was Professor of Zoology at the University of Istanbul, Turkey, when this paper was written. The author adds: "The results presented above are, to a great extent, based upon new records obtained in the course of many excursions into different regions of Anatolia during 17 years. The material help liberally granted by the Rectorate of the University of Istanbul and the Decanate of the Faculty of Science facilitated these scientific trips. In the course of our travels we found the local State authorities of the greatest understanding and readiness to help whenever required. I wish to express to them our gratitude in the name also of my collaborators who participated in these excursions. Wherever we came we were deeply impressed by the generous hospitality with which we were honoured even in the most remote villages of the country. Our task could not have been completed without the sincere interest shown by many private people all over Anatolia."

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